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Species boundaries, biogeography, and intra-archipelago genetic variation within the Emoia samoensis species group in the Vanuatu Archipelago and Oceania

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SPECIES BOUNDARIES, BIOGEOGRAPHY, AND INTRA-ARCHIPELAGO GENETIC VARIATION WITHIN THE *EMOIA SAMOENSIS* SPECIES GROUP IN THE VANUATU ARCHIPELAGO AND OCEANIA

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ABSTRACT

Speciation, geographic variation, and genetic differentiation are fundamental processes that generate diversity, and understanding these processes are major goals of evolutionary biology. Evolutionary phenomena may be more observable on islands as compared to continental landmasses as a result of small population sizes, unoccupied niches, and the relative simplicity of island systems and their populations: physical isolation, shorter (and often well documented) geologic time scale, reduced faunal diversity, and lack of outside faunal influence. Yet, despite their incredible diversity, Pacific island faunas have received little research attention relative to other tropical regions. Using molecular data from several species of scincid lizards in the genus *Emoia*, I test hypotheses related to the generation and maintenance of biodiversity in Pacific oceanic systems, examining historical patterns of colonization, dispersal, and differentiation for a member of a vertebrate family with a broad distribution in the islands of the Pacific. This research is primarily conducted within the Vanuatu Archipelago, an ideal island group in which to examine questions associated with the role of island systems in promoting diversification and speciation. Vanuatu is an oceanic archipelago and its fauna is derived either via over water dispersal or cladogenesis. As it is also a geologically young island group (most islands emergent < 2 mya) interpretation and analysis of intra-archipelago variation during the early stages of a radiation are possible from data collected in this system. Comparison of patterns of diversification and differentiation recovered from *Emoia* in Vanuatu with patterns recovered for species in other well-studied, older island radiations (such as the Hawaiian Islands) enables an understanding of the generality of factors promoting diversity and speciation in island systems.

CHAPTER 1: INTRODUCTION

Speciation, geographic variation, and genetic differentiation are fundamental processes that generate diversity, and understanding these processes are major goals of evolutionary biology. Since the voyages of Darwin and Wallace, oceanic islands have been fundamental to the development of the fields of evolutionary biology and biogeography. Oceanic island systems have served as 'natural laboratories', allowing biologists to develop and test hypotheses related to the mechanisms responsible for speciation and extinction. Evolutionary phenomena may be more easily observable on islands than continental landmasses as a result of small population sizes, unoccupied niches (Ziegler 2002), and the relative simplicity of island systems and their populations: physical isolation, shorter (and often well documented) geologic time scale, reduced faunal diversity, and lack of outside faunal influence.

The Pacific Ocean is earth's largest geographic feature, and the islands of the Pacific Ocean have been identified as a 'megadiverse hotspot' with high levels of endemism (Mittermeier et al. 1998b; Myers et al. 2000). Despite their incredible diversity, Pacific island faunas have received little research attention relative to other tropical regions. In this dissertation, I test hypotheses related to the generation and maintenance of biodiversity in Pacific oceanic systems using molecular data. Specifically, I examine historical patterns of colonization, dispersal, and differentiation for a member of a vertebrate family with a broad distribution in the islands of the Pacific.

Most Pacific islands east of New Guinea are oceanic in origin and formed as a result of seamount volcanic activity. Therefore, none of these oceanic islands have ever been connected to continental landmasses. Due in part to their location, the origin of the biota of the oceanic islands in the southwest Pacific Ocean is of great interest, since they are built entirely as a result

of colonization from neighboring sources and differentiation of populations isolated on these islands (Heaney 2000). The abundance and diversity of plants and animals on Pacific oceanic islands is influenced by many factors, including island size, island isolation (MacArthur and Wilson 1963, 1967), and island age and origin. Because of their isolation and lack of a historical connection to the mainland, the fauna of many Pacific islands does not contain the same diversity as adjacent mainland areas; faunal groups are either under or over-represented on oceanic islands depending upon their dispersal ability.

GEOLOGY OF THE VANUATU ARCHIPELAGO

The Vanuatu Archipelago is one component of an island arc system that extends from New Britain to the Solomon Islands and also includes Fiji, Tonga, Vanuatu, and the Kermadec Islands and formed as early as the Cretaceous, (Carney et al. 1985). Vanuatu was originally located a few hundred kilometers further to the northeast, directly between the Solomon Islands and Fiji, and it has been suggested that Vanuatu played a significant role for biota colonizing the southwest Pacific. Vanuatu may have acted as a stepping-stone for Australasian flora and fauna from New Guinea and Australia (Fig. 1.1), enabling many taxonomic groups to reach Fiji and the islands east of Fiji (DeBoer 1995). However, a reversal in polarity of the Fiji and Vanuatu section of the arc 8-10 mya caused Vanuatu to migrate southwest (Malahoff 1982; Carney et al. 1985). This rotation of the Vanuatu Archipelago removed it from the colonization pathway of Fiji from the Solomon Islands and created the North Fiji Basin. Breakup of the arc contributed to the diversity of the region by promoting vicariant speciation events (DeBoer 1995). The current geology of the Vanuatu Archipelago results from three distinct volcanic provinces (Macfarlane et al. 1988). Each province has resulted in the formation of several islands within the archipelago, and is associated with the movements of particular structural entities (such as crustal ridges or frontal arc movements) that create volcanism and island formation (Carney et.

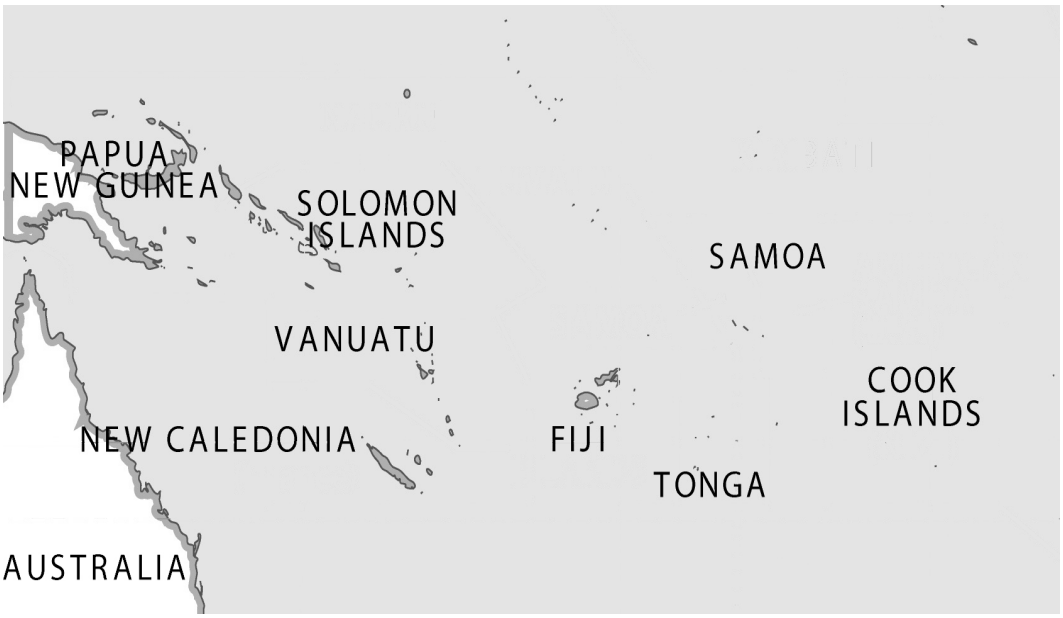

Figure 1.1. The Pacific Ocean showing the location of the major island groups discussed in this dissertation.

al. 1985). The oldest islands in the Vanuatu Archipelago are Espiritu Santo, Malakula, and the Torres Islands (those of the Western Belt), which date from a period of volcanism in the Miocene (11-14 mya). Formation was followed by periods of uplift and erosion, and these islands likely became emergent within the last 2 mya (Carney et al. 1985; Greene et al. 1988b; Macfarlane et al. 1988). The islands of Pentecost and Maewo (Eastern Belt) formed next, resulting from a period of volcanism 14-8 mya. During the late Miocene (8-6 mya) these islands rapidly evolved as a result of sea floor spreading, and likely emerged after 1.8 mya (Carney et al. 1985). The majority of islands in the archipelago belong to the Central Belt. These islands were formed as a result of a period of volcanism that began as early as 3.5 mya and continues to the present (Carney et al. 1985). The dates of island formation and emergence vary among islands in this belt, but all have become emergent relatively recently, likely in the last million years.

The Vanuatu Archipelago is an ideal island group in which to examine questions associated with the role of island systems in promoting diversification and speciation. Vanuatu is an oceanic archipelago and its fauna is derived in two ways: (1) over water dispersal and (2) cladogenesis. This is a geologically young island group (most islands emergent < 2 mya), permitting interpretation and analysis of intra-archipelago variation during the early stages of a radiation. The structure of the Vanuatu Archipelago also lends itself to an examination of the role of factors such as island size, age, isolation, and habitat diversity on population differentiation and speciation as it contains multiple islands of the same approximate ages that differ in size, elevation, or degree of isolation (Fig.1.2). Additionally, the history of sea-level changes and previous connections among islands during periods of lowered sea levels is relatively well known (Dickinson 2001; Mead et al. 2002).

STUDY TAXA

Lizards, particularly the members of the family Scincidae, are conspicuous members of most Pacific island faunas and occur on nearly all Pacific islands (Adler et al. 1995; Gibbons 1985). Within the Scincidae, the genus *Emoia* represents an important component of the terrestrial vertebrate fauna for the islands of the Pacific Ocean. Eleven species of *Emoia* occur in the Vanuatu archipelago, 45% of the species of *Emoia* in Vanuatu are endemic, and 27% of the *Emoia* in Vanuatu have distributions restricted to a single island in the archipelago.

The most recent and significant review of the taxonomy, biogeography and morphology of this genus included 72 species (Brown 1991), although more recent work has indicated that the true diversity of this genus may be much greater, as morphological and molecular evolution have been suggested to be uncoupled in Pacific and southeast Asian skinks (Bruna et al. 1995; Bruna et al. 1996b; Zug and Gill 1997; Austin and Zug 1999; Schmitt et al. 2000) and new species of *Emoia* continue to be identified through ongoing collecting in the Pacific (Ineich 1987; Ineich and Zug 1991; Guillaume et al. 1994; Zug and Ineich 1995). Using morphological characters, Brown (1991) subdivided *Emoia* into eight species groups, which he suggested represent distinct evolutionary lineages.

Five of the eight species groups named by Brown (1991) occur on the islands of the southern Pacific Ocean. Two of these, the *Emoia atrocostata*-group (*E. atrocostata*) and the *Emoia cyanogaster*-group (*E. cyanogaster*), are species-rich groups with the majority of the diversity elsewhere and only a single representative from each group occurring in Oceania. The two species of terrestrial leaf litter skinks that make up the *Emoia adspersa*-group are restricted to the Samoan and Tongan Islands (Brown 1991). The *Emoia cyanura*-group consists of small (adults 37-65 mm SVL), striped lizards predominately found on the forest floor, and on the

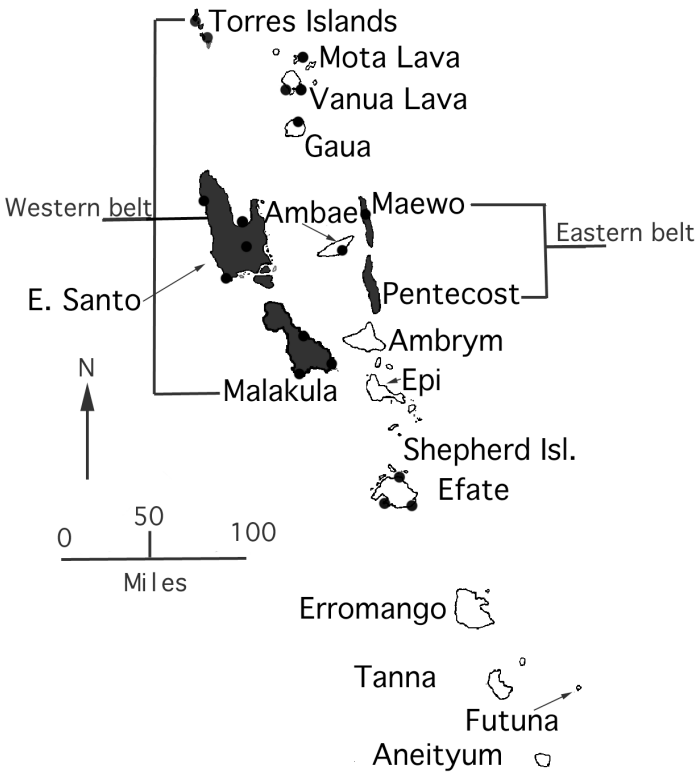

Figure 1.2. Map of the Vanuatu Archipelago, with the three volcanic provinces shown. The islands of the Western Belt (Torres Group, Espiritu Santo, and Malakula) are the oldest islands, followed by the Eastern Belt islands of Maewo and Pentecost. All other islands are part of the Central Chain, and result from the most recent volcanic activity.

ground in more open habitats. Although represented by only three species in Oceania (the majority of the species diversity is in the Solomon Islands), *cyanura*-group skinks dominate numerically, with densities in excess of 4000 individuals/ha (Zug 1991), and are the most widespread, occurring in the Philippines, Indonesia, and from New Guinea throughout the islands groups of the Pacific Ocean (Brown 1991).

In contrast, the *Emoia samoensis*-group is diverse in Oceania and is distributed the Solomon Islands southeastward to Vanuatu and the Loyalty Islands and eastward to the island groups of Fiji, Tonga, and Samoa (Fig.1.1). Of the 13 species assigned to this group by Brown (1991), 11 species have distributions restricted to Vanuatu, Fiji, Tonga, Samoa, and the Cook Islands (Fig. 1.1). *Emoia samoensis*-group species account for 60% of the *Emoia* species occurring within the Vanuatu archipelago, and 30% of the total native lizard fauna of the Vanuatu archipelago. This species group has undergone a radiation within the islands of Oceania; many *samoensis*-group species are endemic to a single archipelago and several have distributions restricted to a single island.

Most members of the *Emoia samoensis*-group are relatively large (adults 52-122 mm SVL) and stout-bodied, highly arboreal skinks, commonly observed basking as high as 20m (Schwaner 1979). There is not much known about the ecology of the members of this species group, but the diet of *E. nigra* (a predominately terrestrial member of this group with significantly broader distribution than any other *samoensis*-group member) consists of wide diversity of invertebrates and other lizard species in Samoa and was found to forage on or near the ground (Schwaner 1979). Another Samoan species, *E. samoensis*, has a more restricted diet of beetles, leafhoppers, caterpillars, and a diversity of plant materials and fruits forages under bark and in trees and shrubs (Schwaner 1979). Both species were found to bask in the morning,

and become active and forage around mid-day, and *E. samoensis* was found to bask again in the late afternoon (Schwaner 1979); several species of arboreal *samoensis*-group skinks in Vanuatu have been observed to have daily activity patterns similar to that reported for *E. samoensis* (Hamilton, personal observation). Clutch size ranges from 2-7 eggs for species within the *samoensis*-group (Schwaner 1979, 1980; Brown 1991; Hamilton et al. 2008a).

Much of the diversity in these predominately arboreal, primarily robust and large-bodied *samoensis*-group skinks was unrecognized until the last four decades. For much of the twentieth century these 11 southern Pacific island species of arboreal skinks were considered a single species, *Emoia samoensis*. Evaluation of island populations of widespread "species" within this group has lead to the description of several new species within the last 20 years. In his systematic review of *Emoia*, Brown (1991) described *E. erronan* from specimens in the AMNH collection. Based on the morphological distinctiveness of these specimens, *E. erronan* was described as a unique taxon endemic to the island of Futuna in the Vanuatu archipelago, and categorized as a member of the *E. samoensis*-group. Continued collection efforts and morphological and molecular investigation into the status of island populations since the work of Brown has lead to the identification of unrecognized species within the *Emoia samoensis*-group (Zug and Ineich 1995), making the actual diversity of this group greater than previously suggested.

CHAPTER 2: ISLAND AREA AND SPECIES DIVERSITY IN THE SOUTHWEST PACIFIC OCEAN: IS THE LIZARD FAUNA OF VANUATU DEPAUPERATE?*

The relationship between species richness, island area, and island isolation is one of the most fundamental models in ecology and biogeography (Arrhenius 1921; Gleason 1922; Preston 1962; MacArthur and Wilson 1963, 1967). In general, faunas show increasing diversity with an increase in area and proximity to the mainland or faunal source. This general pattern, the Species-Area Relationship (SAR), has been key in the development of several fields, including meta-population biology (Gilpin and Hanski 1991) and macroecology (Brown 1995), has been applied to conservation planning (Schafer 1990), and used to model extinction probabilities in the face of increasing fragmentation (Brooks et al. 1997). The relationship between species richness, area, and isolation has been documented for a wide variety of macro- and micro-biotas occupying continental and oceanic islands as well as terrestrial habitat fragments (Lomolino 2001; Lomolino and Weiser 2001; Kalmar 2006; Peay et al. 2007). Island age may influence diversity: older archipelagos have greater endemism at both specific and supraspecific taxonomic levels resulting from the longer emergent time available for both colonization and phylogenetic diversification (Heaney 2000) Islands, or groups of islands, for which the expectations of the SAR pattern are not met are instructive in assessing the generality of this ecological model, and in understanding the relative importance of factors responsible for generating and maintaining species diversity (Frey et al. 2007; Baldi 2008).

One island group suggested to be an exception to the SAR is the Vanuatu Archipelago, a group of 13 large and 80 small islands in the southwest Pacific Ocean (Fig. 2.1). Summarizing published accounts of the herpetofauna of Vanuatu, Allison (1996) noted that previous researchers had considered the Vanuatu herpetofauna depauperate, in part due to the absence of

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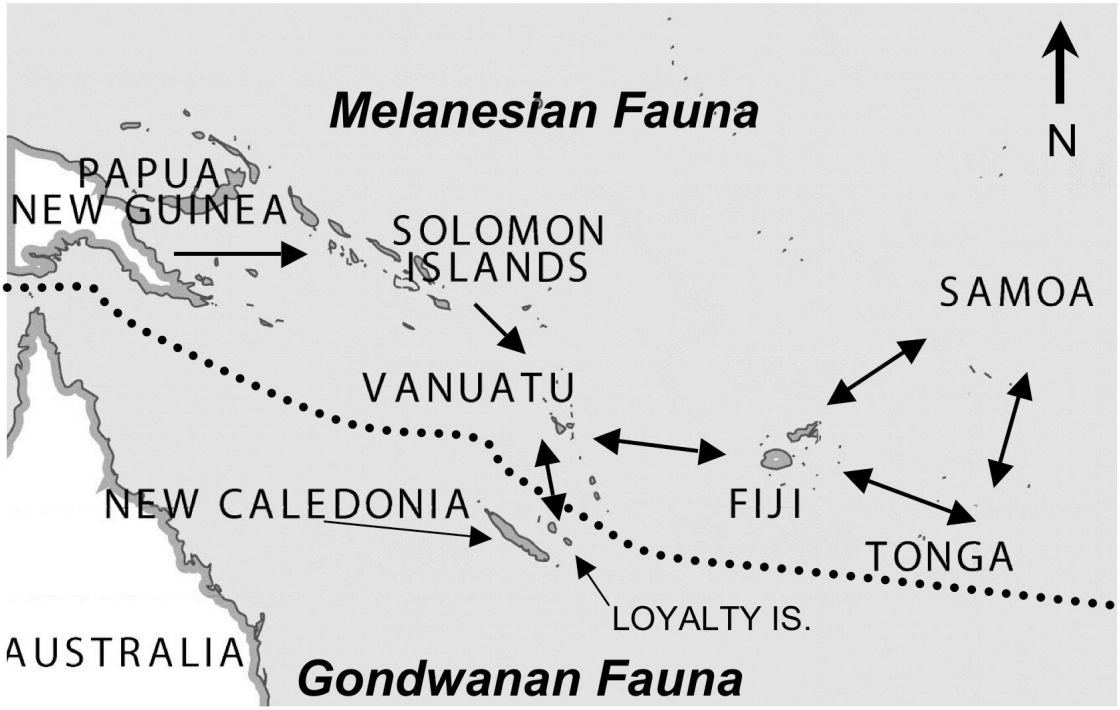


Figure 2.1. Location of the island groups in the southwest Pacific Ocean included in this comparison. Dispersal pathways discussed in this paper are illustrated with arrows. The distribution of the Melanesian lizard fauna (OMA fauna) is depicted with the dotted line; islands to the north of this line have a predominantly Melanesian lizard fauna, whereas those south of the line are derived primarily from a Gondwanan fauna. The fauna of the Loyalty Islands (south of the line) is a mixture of both Gondwanan and Melanesian elements.

endemic snakes and frogs (Baker 1928, 1929; Darlington 1948; Bauer 1988). Additionally, due to the perception that Vanuatu showed low endemism, it has been suggested that much of the species richness in Vanuatu is derived from the Fijian fauna (Gibbons 1985). To test the hypothesis that the lizard fauna of the Vanuatu Archipelago represents an exception to the predictions of the SAR, and thus is depauperate, we compare diversity among several island groups in the southwest Pacific. We also ask whether the inclusion of archipelagos with different faunal sources or geologic origins creates a bias in the perception of the diversity of individual archipelagos.

BIOGEOGRAPHIC BACKGROUND OF THE SOUTHWEST PACIFIC OCEAN

The southwest Pacific Basin is tectonically dynamic, and has resulted in an ever-changing landscape due to mountain building, the formation of new oceanic islands through volcanic activity, and the generation and isolation of continental islands as they are sheared and separated from mainland areas (Carney and Macfarlane 1982; Chase and Seekins 1988). Geologic complexity and dynamically fluctuating landforms are partially responsible for high levels of diversity and endemism in the southwest Pacific (Bauer 1999; Bauer and Sadlier 2000; Myers et al. 2000). Colonization of the island groups in the southwest Pacific and subsequent diversification within these archipelagos must be viewed in light of the geologic history of this region, as historical geology is crucial in understanding the generation and maintenance of diversity of these rich and highly endemic faunas (Parent and Crespi 2006, Gruner 2007, Whittaker et al. 2008).

The geologic process associated with the formation of an island is vital in assessing its diversity and understanding the development of its fauna (Parent and Crespi 2006, Gruner 2007). Oceanic islands result from volcanic sea floor orogeny, with their biota accumulating solely via

over-water colonization and *in-situ* speciation (Carson and Clague 1995, Ziegler 2002). Continental islands, in contrast, are fragments severed from a continental landmass and contain mainland faunas present prior to isolation as well as organisms that have colonized by subsequent over-water dispersal or arose through speciation (Bauer and Sadlier 2000).

Both oceanic and continental islands occur within the geographic region considered in this study (Fig. 2.1). The Fiji archipelago, the islands of Samoa, the Solomon Islands, the Tongan archipelago, and the Vanuatu archipelago are all oceanic in origin, and comprise the majority of the Outer Melanesian Arc (OMA); their development results from tectonic events ranging from 11.2 to 2.0 Mya (Kroenke and Rodda 1984). In contrast, New Caledonia is a continental fragment (Bauer and Sadlier 2000). The Loyalty Islands are a composite of both oceanic and continental elements, with the underlying geology resulting from a continental origin, while the exposed landmass that is the present day Loyalty Islands is coralline in origin and has a history of recent submergence (Bauer and Sadlier 2000); therefore, we consider the Loyalty Islands to be oceanic for the purposes of our analysis. The ages of islands in this study range from approximately 2 Mya (estimated emergence history for groups like Samoa and Vanuatu) to Jurassic (isolation of New Caledonia) (Table 2.1). These archipelagos also vary in isolation from the source area and neighboring island groups, total archipelago land area, and the number, size, and elevation of individual islands within each island group (Table 2.1). The Solomon Islands occur in relatively close proximity to New Guinea, the putative source of much of the archipelago's biota, and have the greatest total land area of all the island groups considered in this study, with four relatively large islands (> 3,000 km^2) and many smaller ones.

In contrast to the archipelagos of the OMA, the histories and geologic origins of New Caledonia and the Loyalty Islands are more complex. New Caledonia is a component of the Inner Melanesian Arc associated with the breakup of Gondwanaland (Bauer and Sadlier 2000).

Table 2.1. Geologic history, size, elevation, and diversity for archipelagos in this study. Diversity is a conservative estimate of true native lizard diversity for each island group. Because of their association with human-modified landscapes, *Hemidactylus frenatus*, *Hemidactylus garnotii* and *Lepidodactylus lugubris* were considered introduced in all island groups. We used personal observations from faunal surveys, unpublished molecular data, personal communications, and literature sources (Appendix 1) to determine species diversity. The primary source for the data on island size and elevation is an online database maintained by the UN Earthwatch Coordination Unit of UNEP (http:// http://islands.unep.ch/isldir.htm) based on data tabulated by Dahl (1986, 1991). Sources for geologic data are provided as footnotes. As the Loyalty Islands and New Caledonia do not have predominantly Melanesian fauna, some comparisons are not relevant and, therefore, omitted.

Island Group	Solomon Islands	Vanuatu Archipelago	Fiji Archipelago	Samoan Islands	Tongan Archipelago	Loyalty Islands	New Caledonia
Geologic Origin	Oceanic	Oceanic	Oceanic	Oceanic	Oceanic	Oceanic	Continental
Emergence History [a]	11.2	2	7.75 [b]	2.75 [c]	14	1.8	150
Total Land Area (km^2)	27,556	12,190	18,272	3,132	699	2,000	17,103
Number of Islands	138	81	322	14	67	8	28
Area of Largest Island (km^2)	5,353	3,955	10,531	1,820	257	1,150	16,760
Islands > 100 km^2	20	14	6	3	2	3	2
Islands >1000 km^2	6	2	2	2	0	1	1
Islands >3000 km^2 [h]	4	1	2	0	0	0	1
Speciation: Immigration Index	44.3	32.4	88.2	0	0	0	97.9
Archipelago Complexity	0.5	0.7	1.8	0.4	9.6	0.4	0.2
Islands with Elevation >500 m	17	19	7	3	1	0	1
Islands with Elevation >1000 m	2	1	3	2	1	0	1
Islands with Elevation >1500 m	2	1	0	1	0	0	1
Maximum Elevation (m)	2,447	1,837	1,324	1,857	1,033	138	1,628
Distance to Faunal Source (km)	710.8	1623.8	2757.4	4040.6	3789.4	2060.6	—
Distance to Neighbor (km)	171.9 (VU)	171.9 (SI)	718.1 (TO)	849.8 (FJ)	718.1 (FJ)	259.3 (NC)	259.3 (LI)
Number of Species	50	20	18	10	14	12	78
Percent of Total OMA Species	68%	27%	24%	14%	19%	—	—
Number of Genera	18	9	8	4	8	7	23
Percent of Total OMA Genera	72%	36%	32%	16%	32%	—	—
Number of Families	4	2	3	3	3	2	3
Number of Endemic Species	29	7	7	2	2	1	67
Endemism Rate	58%	35%	39%	20%	14%	8%	86%

Table 2.1 cont.

Percent of OMA Endemics	62%	15%	15%	4%	4%	—	—
Total No. Species/Emergence	4.46	10.0	2.32	3.64	1.00	6.67	0.52
Number Endemics/Emergence	2.59	3.50	0.90	0.73	0.14	0.56	0.45

[a] Data on island emergence history are from the following: Solomon Islands (Hackman 1973; Kroenke and Rodda 1984); Vanuatu (Greene and Wong 1988; Macfarlane et al. 1988); Fiji (Ewart 1988, Zug 1991); Samoa (Dickinson 2006, Dickinson, pers. comm.); Tonga (Dickinson 2006; Dickinson and Burley 2007, Dickinson, pers. comm.); Loyalty Islands (Kroenke and Rodda 1984, Kroenke 1996, Bauer and Sadlier 2000)

[b] An intermediate date of 7.75 Mya is used; published estimates range from 5.5-10 Mya (Ewart 1988, Zug 1991)

[e] Fragments of present day Upolo and Savai'i date to the late Pliocene to early Pleistocene (2.75-1.55 Mya); the majority of these two islands (as well as all of the Manu'a group) are less than 1.0 Mya, Tutuila dates primarily to the middle Pleistocene, 1.5 to 1.0 Mya (Dickinson 2006).

As the origin of New Caledonia is continental, the biota of New Caledonia does not result primarily from over-water dispersal, unlike other archipelagos considered in this analysis. Since its emergence, New Caledonia has had multiple potential land-bridge connections with Australia and New Zealand (Kroenke 1996; Bauer and Sadlier 2000). The Loyalty Islands are derived from more than a single geological source; some components of this island group are of Gondwanan origin while others are oceanic (Bauer and Sadlier 2000). Additionally, the reptile faunas of New Caledonia and the archipelagos of the OMA are disparate; the reptile fauna of New Caledonia is not predominately Melanesian in origin (Bauer and Sadlier 2000). The biota of the Loyalty Islands is a mixture of Melanesian fauna, derived from New Guinea, and continental Gondwanan fauna derived primarily from New Caledonia and not shared with the oceanic islands of the OMA (Bauer and Sadlier 2000).

The colonization of the Pacific oceanic islands by reptiles is thought to have occurred by way of a stepping-stone route (Fig. 2.1) from the source area of New Guinea into the islands of the southwest Pacific (Brown 1991; Allison 1996), a dispersal pathway also suggested for other fauna (Simpson 1953). Dispersal along this pathway generates the expectation that faunas will become more impoverished eastward with increasing distance from the source region, as organisms with limited vagility are not able to colonize these more remote archipelagos (Crombie and Steadman 1986; Woodroffe 1987). Under this scenario, assuming roughly equal area among all archipelagos, the fauna of the Solomon Islands should be the most diverse because of its proximity to New Guinea. The fauna of the Vanuatu Archipelago should have moderate diversity, as components of the fauna with a more limited ability for over-water dispersal would have been filtered out during dispersal from New Guinea via the Solomon Islands. Likewise, Fiji should have faunal diversity lower than the Vanuatu Archipelago, as dispersal to Fiji from New Guinea occurred by way of the Solomon Islands and Vanuatu, with

each archipelago acting as both stepping-stone and faunal filter (Fig. 2.1). The most remote island groups in this study, Tonga and Samoa, should have the lowest faunal diversity, as fewer species would have dispersal capabilities great enough to colonize these archipelagos (Fig. 2.1).

MATERIALS AND METHODS

To determine whether the lizard fauna of the Vanuatu Archipelago represents an exception to the SAR, we examine the species-level lizard diversity of the Vanuatu Archipelago and compare this to neighboring island groups. We have restricted this comparison to lizards because they are one of the most diverse terrestrial vertebrate groups throughout the Pacific. In addition, lizards possess three other characteristics that make this group well-suited for studies of Pacific island biogeography: (1) they have moderate vagility, i.e., intermediate between organisms with extremely limited over-water dispersal ability (amphibians) and highly vagile groups (birds); (2) they are conspicuous members of the fauna of Pacific islands and are relatively easy to survey; and (3) the contemporary distribution of lizard faunas in the Pacific does not result primarily from anthropogenic causes. In contrast, recent evidence from mammals and birds has shown that the modern distributions and consequent patterns of species diversity of these two vertebrate groups have been drastically altered by human-mediated introductions and extinctions (Pregill and Dye 1989; Steadman 1995; Matisoo-Smith et al. 1998; Steadman et al. 1999; Steadman et al. 2002b). We considered a species introduced if a previous worker indicated that the distribution was likely the result of introduction and provided supporting data (Appendix 1).

To evaluate whether the lizard fauna of Vanuatu is an exception to the diversity patterns expected under the SAR, we used the model of MacArthur and Wilson (1967) to predict numbers of species (S) occurring in each archipelago:

$$\log S = z \log A + \log c \quad \text{or} \quad S = cA^z$$

where S = number of species, A = area, c = intercept of the y-axis, z = slope of the relationship

between (log) species richness and (log) area. We compiled species lists (Appendix 1) for each island group using available literature sources and personal field observations and determined the number of species endemic to each island group. It is important to note that our understanding of the reptile faunas of these archipelagos is still incomplete; for example, 20 species of lizards have been described from the southwest Pacific since 2000 (Appendix 1). We included all published species as of 1 August 2008. We considered a species endemic if its distribution was restricted to a single archipelago or island group. We compared diversity values calculated under the expectations the SAR to native lizard diversity in each island group. The proportion of the overall OMA lizard diversity that occurs in Vanuatu was compared to the proportion that occurs in the Solomon Islands, Fiji, Samoa, and Tonga. Four measures of diversity were calculated for each archipelago: (1) representative species diversity- the number of species in each island group / the total number of OMA species; (2) representative generic diversity- the number of genera in each island group / the total number of OMA genera; (3) representative endemism- the number of species endemic to each island group / the total number of species endemic to a single archipelago within the OMA; and (4) percent endemism- the percentage of an island group's fauna that is endemic to that island group. These diversity measures, as well as total number of species, genera, and endemic species occurring in each archipelago, were regressed against three factors suggested to be important in predicting species richness: total archipelago area, archipelago age (based on the earliest date of continuous emergence), and isolation using SAS. Island age data were determined from the literature, and the source for each island group is provided in Table 2.1. Data on island size and elevation are from an online database maintained by the UN Earthwatch Coordination Unit of UNEP (http://islands.unep.ch/isldir.htm) based on data tabulated by Dahl (1986, 1991). We used 'total land area' as our value for archipelago area. We used the Lambert Conformal projection for the

southwestern Pacific in ArcGIS to calculate two separate measures of isolation: 1) distance from the faunal source and 2) distance from the nearest neighbor. Distances were measured as a straight-line distance from the most adjacent points of neighboring islands. For example, to calculate distance from the faunal source (New Guinea) to Vanuatu, we compared multiple straight-line distances between the southeastern tip of New Guinea, Milne Bay Province, and the northernmost islands in Vanuatu, the Torres Island group. The shortest distance between these points was used. Due to the small number of data points we did not expect these relationships to be statistically significant, but R^2 values allow us to make cautious inferences about the relative strength of various relationships.

To examine the relationship between species diversity, endemism, and biogeographical factors not explicitly considered in the SAR, we generated two additional measures of archipelago features for comparison among island groups, as attributes of islands themselves may influence species diversity, community composition, and speciation in divergent ways (Parent and Crespi 2006). The result of these divergent processes generates variation in the relative roles of within-island speciation, interisland speciation, and immigration in shaping the species richness of an island or archipelago (Losos and Schluter 2000, Parent and Crespi 2006). Based on the observation that 3000 km^2 is a critical size for islands above which the rate of within-island speciation exceeds the rate of immigration (Losos and Schluter 2000), we calculated a Speciation: Immigration index. This index is simply a measure of the amount of overall archipelago area that consists of islands large enough so that the within-island speciation rate would be predicted to exceed the immigration rate (Losos and Schluter 2000). We expect this measure to be positively correlated with the rate of endemism. The Speciation: Immigration index is calculated as:

[Total area of islands (km^2) > 3000 km^2 / total archipelago area (km^2)] x 100

The structure of an archipelago is expected to influence the generation of diversity as well; small peripheral islands adjacent to a much larger island would be expected to result in a different fauna than several large islands lacking small peripheral islands between them. To examine the differences in species diversity and endemism associated with the structure of archipelagos, we calculate a second measure, Archipelago Complexity. Archipelago Complexity provides a way to examine the structure of the archipelago in terms of the number of islands, when controlling for the overall area of an archipelago. A higher value indicates a greater number of smaller islands, whereas a low number would indicate that the majority of land area in the archipelago is contained within a lower number of large islands. Archipelago Complexity is calculated as:

[Total number of islands (km^2) / total archipelago area (km^2)] x 100

We consider archipelagos rather than individual islands within archipelagos as our unit of comparison for two primary reasons. First, the island groups in this analysis are remote and have historically been poorly studied. As a result of this, for many islands species lists are either not available or are expected to not be sufficiently comprehensive. Second, as the distance among islands within an archipelago is significantly less than the distance between any of the archipelagos considered in this study, we consider each archipelago to function as a biogeographic unit. Because we were interested in comparing diversity among archipelagos, we considered A = total archipelago area.

In the SAR, the rate at which species richness accumulates with an increase in area is the slope of the relationship between (log) species richness and (log) area, and is represented in the equation as *z*. Preston (1962) found $z = 0.301$ for amphibians and reptiles in the West Indies, and subsequent work has suggested that, for islands, the value of *z* is generally around 0.30 and does not vary greatly among taxa or with geography (MacArthur and Wilson 1963, 1967; Lomolino

2001). Based on these previously reported values of z, we used $z = 0.30$ in our calculations. Because the value of z can influence the predicted species richness of an area, we used one value for z across archipelagos to reduce bias.

To determine what value to use for c (the value of the y-axis intercept in the SAR), we estimated the likely range of c-values from lizards distributed in other Pacific archipelagos (Table 2.2). Specifically, for these archipelagos we generated estimates of c using the SAR. We took the number of species (represented by S) and area (A) reported in the literature, and a z value of 0.30 as previously explained. Using the SAR, we solved for c for each island group. The obvious problems inherent in computation of c values from literature sources, such as the likelihood of incomplete faunal lists or erroneous data, make these values appropriate only as a guideline for generating a value of c for our islands and taxa of interest. We do not expect *a priori* the five island groups considered in this analysis to have identical c values as c is influenced by isolation (MacArthur and Wilson 1967; Lomolino 2001), and degree of isolation and distance from potential source populations vary greatly among the island groups in our analysis. The relative strength of the influence of isolation or environmental quality on the parameter c is unclear. Therefore, we used a single c value for all island groups considered in this analysis. We used $c = 2.13$, the mean of the c-values for lizard species from other Pacific archipelagos (Table 2.2). We generated an estimate of error ($c \pm 2.45$) equal to two standard deviations of the mean c-value and estimated potential diversity for each island group for $c \pm 2.45$.

Our primary analysis is restricted to five island groups (Fiji, Vanuatu, the Solomon Islands, Samoa, and Tonga) for three reasons: (1) these archipelagos result from the same general geologic processes (oceanic origin) and are components of the OMA (Bregulla 1991, Zug 1991, McCoy 2006); (2) none of these archipelagos have a confounding historical association with the

Table 2.2. *C* values for lizards from other Pacific islands and archipelagos from literature sources. These *c* values are used as a guideline in the selection of a value for *c* for our analysis, and in the generation of a set of confidence intervals.

Archipelago	Species	Area (km^2)	*c*	Source
Admiralty Islands	30	2,072	3.0	Allison 1996
Bismarck Islands	40	49,700	1.6	Adler et al. 1995
Kapingamarangi Atoll	4	1.3	3.7	Buden 1998
Marshall Islands	9	181	1.9	Adler et al. 1995
Mariana Islands	5	471	0.8	Adler et al. 1995
Mortlock Islands	9	12	4.3	Buden 2007a, 2007b
New Britain	32	39,807	1.3	Allison 1996
New Ireland	23	7,405	1.6	Allison 1996
Niue	5	259	0.9	Adler et al. 1995
Palau	23	415	3.8	Crombie and Pregill 1999
Pitcairn Islands	3	43	1.0	Gill 1993b
Wallis and Futuna	8	177	1.7	Gill 1995

mainland or with each other (Bregulla 1991, Zug 1991, McCoy 2006); and (3) these archipelagos all have the same putative faunal source (Allison 1996). This third point (faunal source) is especially critical, as it eliminates the possibility that differences in lizard species richness recovered in these archipelagos are a result of differences in richness among source faunas or variation in dispersal capacity (as a result of phylogenetic constraint or other factors) among source populations. The inclusion of neighboring island systems enabled a comparison of islands of differing sizes, geologic histories, degrees of isolation, and proximity to source populations.

To understand the influence of inclusion or exclusion of island groups in this analysis, we performed these same comparisons including two additional island groups: New Caledonia and the Loyalty Islands. Despite their geographic proximity, New Caledonia and the Loyalty Islands differ from the OMA archipelagos with respect to geologic history, patterns of colonization, and faunal origin.

RESULTS

There is a positive relationship between total archipelago land area and species richness (Fig. 2.2), as predicted by the SAR. The species diversity of New Caledonia and the Solomon Islands exceeds the level of species diversity predicted by archipelago area alone, and all other island groups (Samoa, Tonga, Fiji, Vanuatu and the Loyalty Islands) have fewer species than expected (Fig 2.2). For all island groups analyzed, however, observed species richness falls within the 95% confidence intervals (Fig. 2.2).

Archipelago area is a relatively good, but not statistically significant, predictor of the proportion of OMA species (R^2= 0.75, p=0.059) and OMA endemics (R^2= 0.78, p=0.046) that occur within an archipelago (Table 2.3); the diversity of both OMA species and OMA endemic species increases with area (Fig. 2.3a). The Solomon Islands, and perhaps Tonga, appear to have

a greater proportion of OMA diversity than predicted by this relationship, and the diversity in Fiji appears lower than expected (Fig. 2.3a). Both Vanuatu and Samoa appear to have roughly the level of OMA diversity that would be predicted by the total Archipelago Area (Fig. 2.3a). The relationship between these measures of diversity and archipelago emergence history is very weak; island emergence history is a poor predictor of the proportion of OMA lizard fauna present in an archipelago (Table 2.3). In general, older archipelagos tend to have greater diversity (Fig. 2.3b), although there are clear exceptions (i.e., Tonga). The proportion of OMA species and endemics decreases with both distance from the faunal source of New Guinea (Fig. 2.3c) and the nearest neighbor (Fig. 2.3d); proximity to the faunal source explains more of the variation in diversity for OMA species and OMA endemics than the proximity of the nearest neighbor, but these relationships are not statistically significant (Table 2.3). The Solomon Islands appear to have a greater component of both OMA species diversity and OMA endemism than this relationship predicts, and the OMA lizard diversity appears to be lower than expected for Vanuatu based on its proximity to the faunal source of New Guinea (Fig. 2.3c), and the Solomon Islands, its nearest neighbor (Fig. 2.3d).

A positive, statistically significant relationship was found between the endemism rate of an archipelago and the size of the largest island (Fig. 2.4a; Table 2.3); the relationship between endemism rate and the Speciation: Immigration Index was also positive, but was not statistically significant after $\propto$ was adjusted using a sequential Bonferroni (Fig. 2.4b; Table 2.3). Vanuatu had a higher endemism rate than expected when either the size of the largest island (Fig. 2.4a) or the Speciation: Immigration Index (Fig. 2.4b) were considered. Based on the size of the largest island in an archipelago, Vanuatu, the Solomon Islands, and New Caledonia appear to have greater diversity than predicted, the Loyalty Islands and Fiji appear to have lower diversity than expected, and the diversity of Samoa and Tonga meet predicted values (Fig. 2.3a). A similar

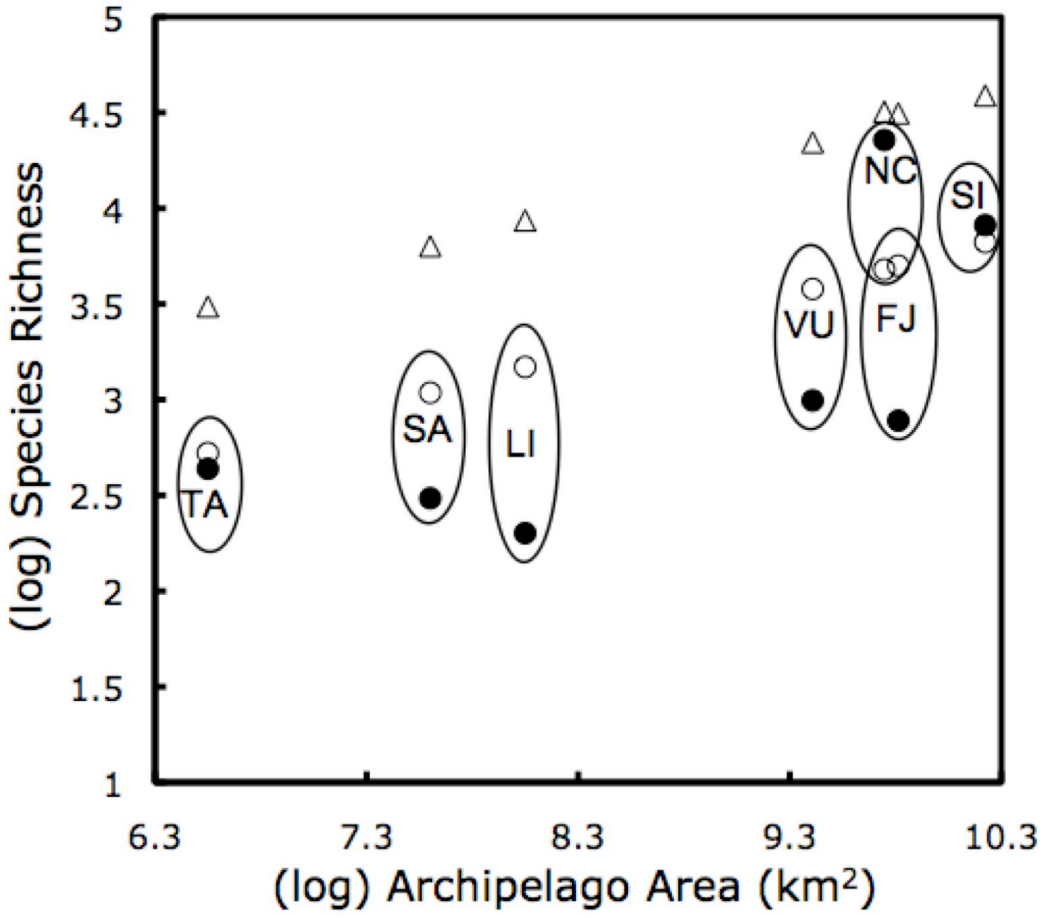


Figure 2.2. Observed lizard species richness (closed circles) for each island group and the lizard species richness (open circles) for each group expected under the Species–Area Relationship (SAR). Expected values were calculated using a value of 2.13 for the parameter *c*. The 95% maximum confidence interval (triangles) was calculated with $c \pm 2.45$, which is the mean value of *c* for reptiles in other Pacific island groups ± two standard deviations (see Table 2). Minimum confidence intervals are not shown, as they are zero for all island groups in this study. Archipelago abbreviations: Fiji (FJ), Loyalty Islands (LI), New Caledonia (NC), Samoa (SA), Solomon Islands (SI), Tonga (TO), and Vanuatu (VU).

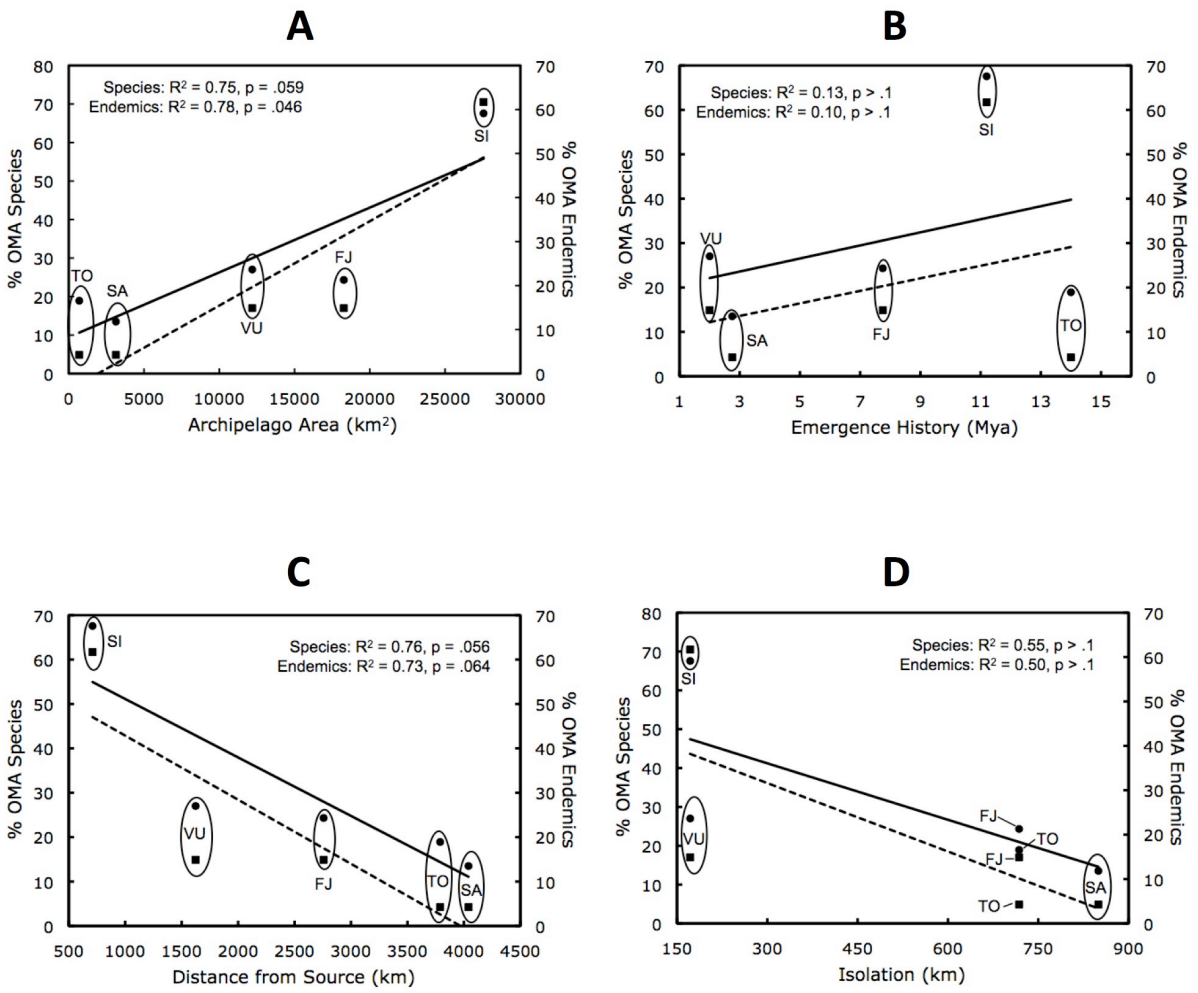


Figure 2.3. The percentage of the total Outer Melanesian Arc (OMA) lizard fauna occurring in each island group and the percentage of the OMA lizard species endemic to each island group. These diversity measures are shown in relation to four archipelago features: (A) total archipelago area (km^2), (B) length of time the archipelago has been continually emergent (Mya) (C) distance from the faunal source of New Guinea (km), and (D) distance from the closest point of the nearest neighboring island group (km). For all panels closed circles represent species richness and closed squares represent the percentage of the endemic lizard fauna restricted to each archipelago. Solid lines are associated with species richness values; dotted lines with percentage of endemic species in each archipelago. Archipelago abbreviations: Fiji (FJ), Loyalty Islands (LI), New Caledonia (NC), Samoa (SA), Solomon Islands (SI), Tonga (TO), and Vanuatu (VU). R^2 values and *p*-values for all regressions are presented in Table 2.3.

Table 2.3. Comparisons of diversity among archipelagos. *Significant when ∝-level of 0.05 is adjusted using the sequential Bonferroni correction (Rice 1989). Strongest predictor for each measure of diversity is highlighted in bold, even if the relationship is not statistically significant at the adjusted ∝-level.

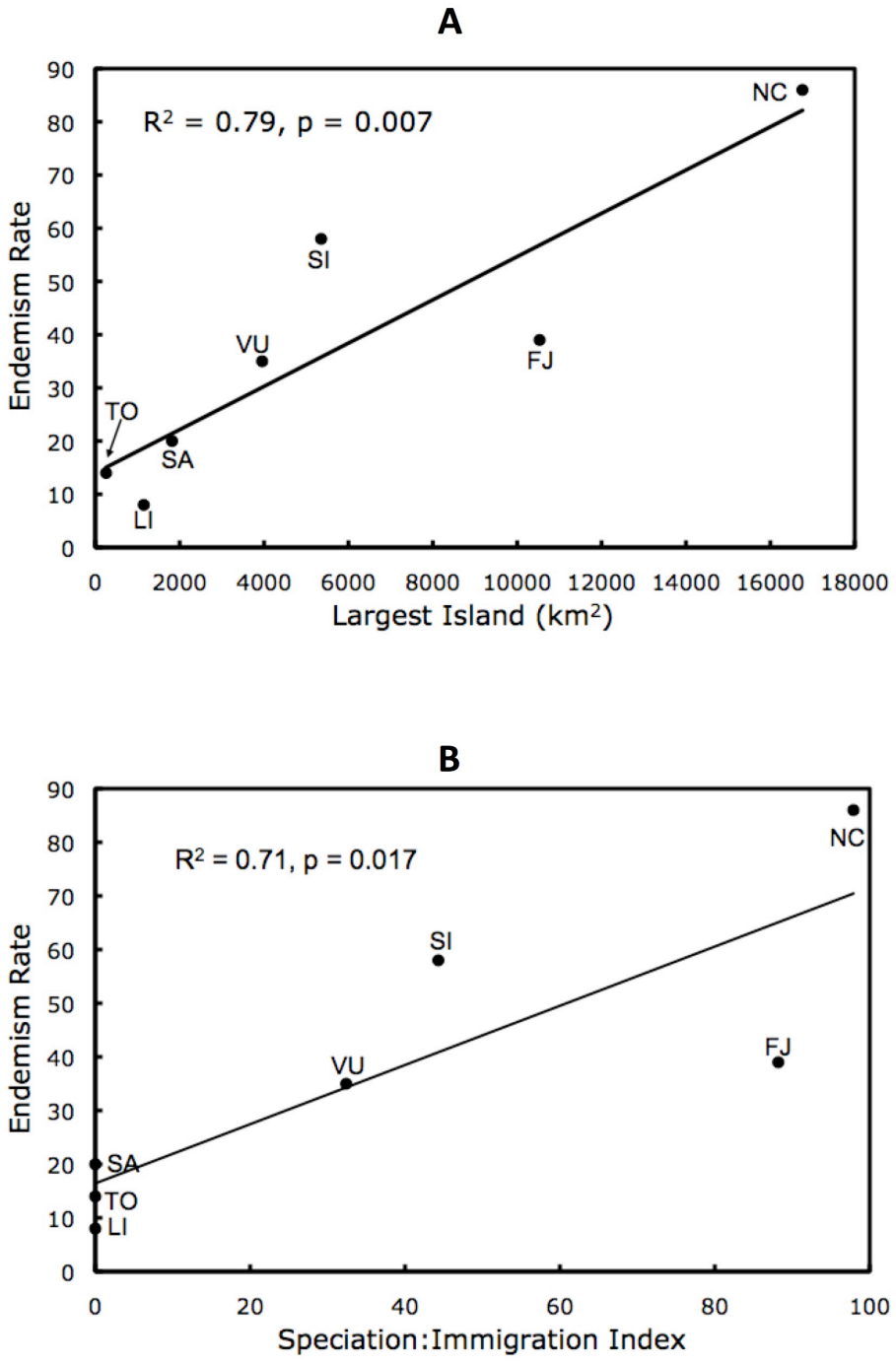
Diversity measure	R^2	*p*	Figure
Percentage of OMA Species Present			
Archipelago area	**.75**	**.059**	3a
Emergence	.13	>.1	3b
Distance from source	**.76**	**.056**	3c
Isolation	.55	>.1	3d
Percentage of OMA Genera Present			
Archipelago area	**.78**	**.046**	3a
Emergence	.10	>.1	3b
Distance from source	.73	.064	3c
Isolation	.50	>.1	3d
Endemism Rate			
Size of largest island	**.79**	**.007***	4a
Speciation: Immigration index	.71	.017	4b
Total Number of Species			
Maximum elevation	**.54**	**>.1**	5c
Size of largest island	.07	>.1	5e
Total Number of Endemic Species			
Maximum elevation	**.59**	**>.1**	5d
Size of largest island	.10	>.1	5f

pattern is seen with respect to the Species: Immigration Index: the Solomon Island and New Caledonia appear to have elevated diversity, Fiji and the Loyalty Islands appear to show reduced diversity, and Vanuatu, Samoa, and Tonga seem to meet the predictions of this model (Fig 2.4b).

When the number of species and the number of endemic species in an archipelago are compared with respect to archipelago area (Figs. 2.5a,b), maximum elevation (Figs. 2.5c,d), and size of the largest island (Figs. 2.5e,f), the relationship between diversity and archipelago features is stronger, but not statistically significant, when the analysis excludes islands that do not share a faunal source and geologic origin (Figs. 2.5a-d). The addition of New Caledonia and the Loyalty Islands improves the relationship between the size of the largest island and the total number of species (Fig. 2.5e) and endemic species (Fig. 2.5f) in an archipelago. The islands included in an analysis have an affect on the perception of diversity within an island group (Fig. 2.5); Tonga and Fiji appear to have lower diversity than would be expected by the maximum elevation if the analysis contains all islands; when the analysis is restricted to OMA archipelagos, Fiji and Tonga appear to be more diverse than expected (Figs. 2.5c,d).

There is a clear difference in lizard species diversity between the Solomon Islands, a large archipelago (50 native species), and the smaller archipelagos of Vanuatu (20), Fiji (18), Tonga (14), the Loyalty Islands (12), and Samoa (10). The highest lizard species diversity occurs in New Caledonia (78 species). Despite having less total archipelago land area than Fiji, Vanuatu is slightly more representative of the overall OMA lizard diversity, with 27% of the native OMA lizard species and 24% of the endemic species occurring in this archipelago (Fig. 2.3a). The largest component of the OMA lizard fauna occurs in the Solomon Islands; 68% of the OMA native lizard fauna occurs in the Solomon Islands (Table 2.1). Additionally, a large component (58% species-level endemism) of the lizard fauna of the Solomon Islands is endemic (Table 2.1). Endemism is noticeably lower for the other island groups considered in this study:

Figure 2.4. Endemism Rate for each island group in this study when two measures suggested to influence the contribution of speciation relative to immigration in faunal accumulation on islands (Losos and Schluter 2000) are considered: (A) Endemism Rate (the percent of the total archipelago fauna endemic to the archipelago) for each archipelago regressed against the size of the largest island within the archipelago; (B) Endemism Rate for each archipelago regressed against our Speciation: Immigration Index Island groups with a high Speciation: Immigration Index are predicted to have a greater proportion of endemic species. Archipelago abbreviations: Fiji (FJ), Loyalty Islands (LI), New Caledonia (NC), Samoa (SA), Solomon Islands (SI), Tonga (TO), and Vanuatu (VU). R^2 values and *p*-values for all regressions are presented in Table 2.3.


A
R² = 0.79, p = 0.007
NC
SI
VU
FJ
TO
SA
LI
Endemism Rate
Largest Island (km²)
0
10
20
30
40
50
60
70
80
90
0
2000
4000
6000
8000
10000
12000
14000
16000
18000
B
R² = 0.71, p = 0.017
NC
SI
VU
FJ
SA
TO
LI
Endemism Rate
Speciation:Immigration Index
0
10
20
30
40
50
60
70
80
90
0
20
40
60
80
100

Vanuatu (35%) and the Fijian archipelago (39%) have species-level endemism values roughly comparable to each other (Table 2.1). In archipelagos located farther from the source of New Guinea endemism is lower; 20% of the Samoan fauna and 14% of the Tongan fauna are endemic (Table 2.1).

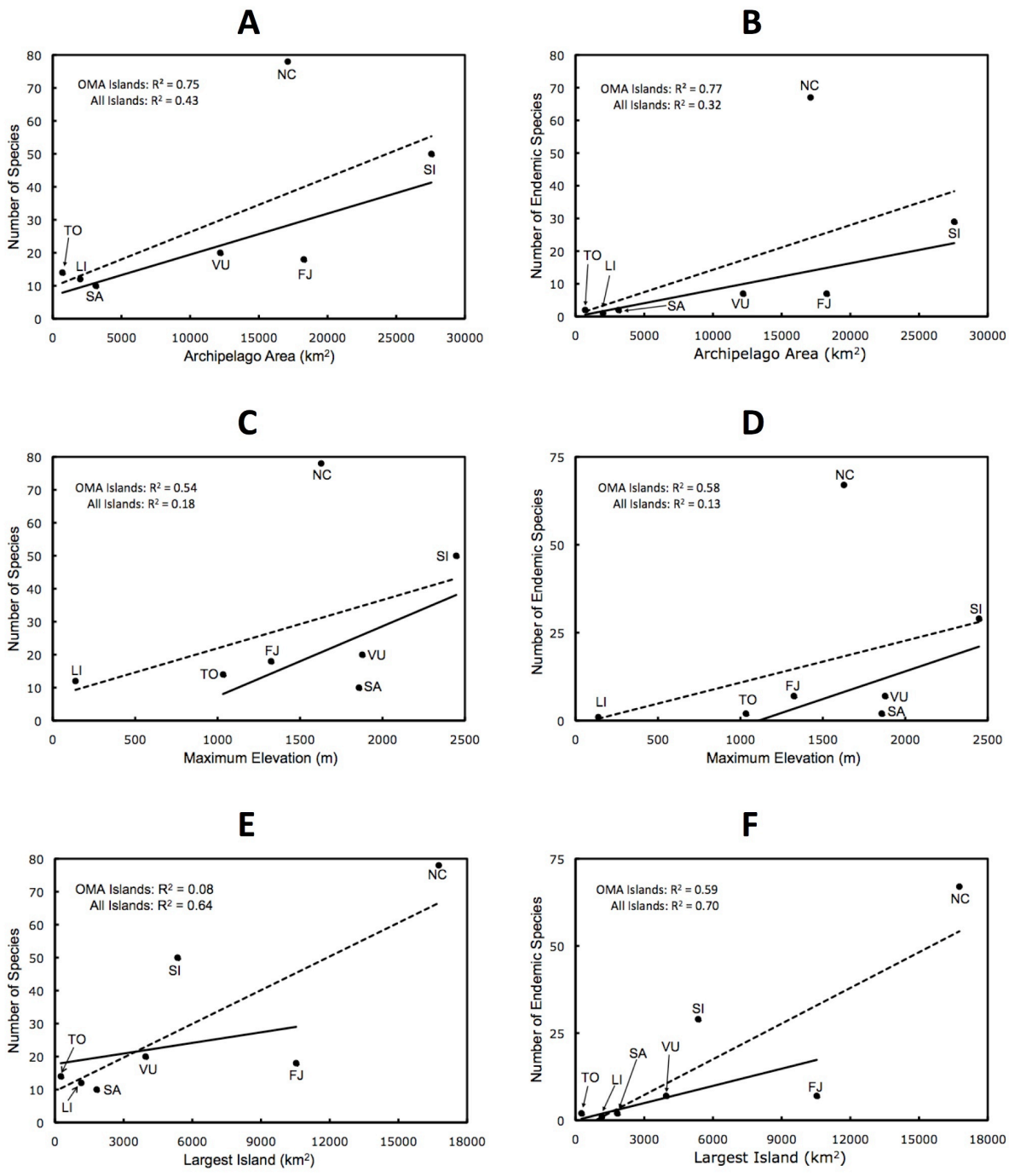
Archipelago complexity ranged from 0.2 (New Caledonia; most of the area restricted to a single, large island) to 9.6 (Tonga; 67 islands, the largest of which is only 257 km^2), and was not correlated with either species diversity (R^2= 0.10, p>0.1) or endemism (R^2= 0.10, p>0.1). Three archipelagos (Samoa, Tonga, and the Loyalty islands) had a Speciation: Immigration Index of 0, as no island in the group was ≥ 3,000 km^2 (Table 2.1). Index values ranged from 32.4 (Vanuatu) to 97.9 (New Caledonia) for the remaining archipelagos. As predicted, endemism was higher in the island groups with higher Speciation: Immigration Index than in the three islands with an Index of 0 (R^2= 0.71, p=0.017; Fig. 2.4b), although this relationship was not statistically significant after ∝ was adjusted using a sequential Bonferroni correction (Rice 1989, Table 2.3).

DISCUSSION

The biotic composition of an island is influenced by myriad factors, including past and present geologic circumstances. Islands with different geologic histories may have drastically different faunas as a result of the influence of island age, timing of island emergence, and mode of island origination. These factors are important in explaining the differences in the composition and species diversity of their lizard faunas, as opportunities for colonization and speciation change through time and space.

The SAR does not consider all the relevant, and perhaps most important, components of biodiversity such as speciation, which is crucial to the evolution of island biotas (Heaney 2000). Because of the isolated nature of oceanic Pacific islands, speciation is essential in the development of island faunas. In addition to speciation, other factors such as island emergence

Figure 2.5. Influence of archipelago inclusion on the perception of diversity in relationship to archipelago area, maximum elevation of an archipelago, and the size of the largest island in an archipelago. Lizard species diversity (A) and endemism (B) within each archipelago shown in relation to total archipelago area. Panels C and D show the relationship between diversity and maximum elevation within an archipelago for both (C) number of lizard species in an archipelago and (D) the number of lizard species endemic to each archipelago. The relationship between diversity and the size of the largest island is depicted in panels E and F: (E) relationship between the size of the largest island in an archipelago and the number of lizards species found in that archipelago, (F) relationship between the size of the largest island in an archipelago and the number of lizards species endemic to that archipelago. For all panels, the solid line represents the relationship between diversity and area when the analysis is excluded to the five archipelagos that share a faunal origin (OMA Islands), whereas the dotted line shows the relationship between diversity and area when New Caledonia and the Loyalty Islands are included (All Islands). R^2 values are shown for OMA Islands and All Islands. Regressions were conducted for the relationships between diversity and OMA Islands with respect to maximum elevation (C & D) and the size of the largest island (E & F); *p*-values are provided in Table 2.3. Other relationships were not evaluated statistically, but their inclusion in this figure allows a visual, qualitative effect of the influence of archipelago choice on the perception of diversity.


A
OMA Islands: R² = 0.75
All Islands: R² = 0.43
Number of Species
Archipelago Area (km²)
NC
SI
TO
LI
VU
FJ
SA
B
OMA Islands: R² = 0.77
All Islands: R² = 0.32
Number of Endemic Species
Archipelago Area (km²)
C
OMA Islands: R² = 0.54
All Islands: R² = 0.18
Number of Species
Maximum Elevation (m)
D
OMA Islands: R² = 0.58
All Islands: R² = 0.13
Number of Endemic Species
Maximum Elevation (m)
E
OMA Islands: R² = 0.08
All Islands: R² = 0.64
Number of Species
Largest Island (km²)
F
OMA Islands: R² = 0.59
All Islands: R² = 0.70
Number of Endemic Species
Largest Island (km²)

history and additional components of archipelago complexity are likely to be significant in determining the species diversity and level of endemism observed on islands (Gruner 2008), and the contemporary fauna must be evaluated in light of these processes. Archipelago complexity, a concept that encompasses disparate components such as the number of islands within an archipelago, the distance among islands, the degree of variation in size and elevation of islands, and even factors influencing dispersal across the archipelago matrix (such as ocean currents and changes in sea level) likely play key roles in shaping patterns of species richness in oceanic archipelagos by influencing colonization, speciation, and extinction. We have attempted to examine the diversity of these archipelagos taking speciation and archipelago complexity into consideration, if only using coarse comparisons. We found the level of endemism in an island group increased as the size of the largest island in the group increased; the size of the largest island accounted for 79% of the observed variation in the level of endemism. The relationship between the proportion of an archipelago that consisted of islands ≥ 3,000 km^2 and archipelago endemism was also positive, and although not significant statistically (p=0.017), explained 71% of the variation and likely represents a biologically relevant relationship. Archipelagos in which a greater proportion of the total area was made up of larger islands (i.e. the Solomon Islands and New Caledonia) had higher endemism, and those with large numbers of small islands and no really large islands (i.e. Tonga and the Loyalty Islands) had lower levels of endemism. As the relationship between size of an island and the relative contribution of immigration and speciation to faunal accumulation has been previously examined for lizards (Losos and Schluter 2000), we did expect to find this positive relationship between island size and endemism.

We attempted to evaluate the role of Archipelago Complexity (AC) on patterns on diversity. We did not expect to see a directional pattern (i.e., smaller value for archipelago

complexity would predict lower diversity, or vice versa) with respect to our crude measure of AC; rather we expected that archipelagos with similar AC values would also have similar endemism rates or other measures of diversity. As this was not the case (Table 2.1), it is likely that our simple measure of AC cannot capture the complex interaction between the relative areas and number of individual islands within an archipelago, as well as the distance among islands and the difficulty in crossing the intra-archipelago dispersal matrix, affected by factors such as ocean currents and historical changes in sea level, resulting in increases or decreases in intra-archipelago distances and in the size of islands themselves. These variables are difficult to quantify, but future studies focusing on insular patterns of species richness should consider the role of archipelago complexity.

Patterns of Southwest Pacific Biogeography

Previous research on patterns of insular diversity in the southwest Pacific indicate a high proportion of the mammal fauna has an Austral-Papuan affinity (Carvajal and Adler 2005), as do lizards. Archipelago species richness of mammals is driven by isolation (negative relationship) and archipelago area (positive relationship) (Carvajal and Adler 2005). The pattern we recovered for lizards was similar; a positive relationship was found between archipelago area and both species diversity and endemism (Figs. 2.2, 2.3a), as well as between endemism rate and the size of the largest island in an archipelago (Fig. 2.4a). We also found a negative relationship between lizard species richness and distance from the faunal source (Fig. 2.3c) as well as distance from the nearest neighboring landmass (Fig. 2.3d), although this relationship was not as strong as distance from the source.

Like lizards, OMA mammals have their highest diversity in the Solomon Islands (Carvajal and Adler 2005). This diversity results from proximity to the faunal source, the relatively larger size of individual islands (promoting both relatively low levels of extinction and

subsequent intra-archipelago speciation). We suggest these same factors generate the higher lizard diversity we report for the Solomon Islands. For both mammals and lizards, intra-archipelago speciation is a significant contributor to the high species diversity and endemism of the Solomon Islands fauna. These patterns are congruent with the idea that larger islands should have greater endemism, and provide partial support for the predictions that endemism should be greatest on larger, isolated islands, and that an insular size threshold exists above which speciation becomes the significant contributor to species diversity (Johnson et al. 2000; Losos and Schluter 2000). Our data, and data for mammals, do not provide support for the relationship between endemism and isolation alone. Island size, rather than isolation, seems to be more important for lizards and mammals, perhaps due to their intermediate vagility. Perhaps there is some lower bound of isolation required to promote speciation by reducing gene flow, likely related to the vagility of the taxon, and some upper bound of isolation above which initial colonization and subsequent extinction become less and more likely, respectively.

Molecular phylogenetic data have recently provided novel insights to the patterns of speciation and diversification within Pacific Island birds. These data revealed two geographically distinct radiations (Filardi and Moyle 2005). One radiation was the historically expected pattern of island taxa resulting from continental forms, whereas the second radiation resulted from diversification occurring on islands within the tropical Pacific. No comparable work has been published for reptiles to allow us to make comparisons with our results, but the patterns of species diversity and high levels of endemism in island groups such as Vanuatu, the Solomon Islands, and Fiji suggest that a similar diversification history may exist for Pacific Island reptiles. Further research on the phylogenetic relationship of Pacific Island lizards is necessary for an accurate assessment of the evolutionary and biogeographic history of these lineages.

Is Vanuatu a Depauperate Outlier?

Lizard diversity in the Vanuatu Archipelago, and all other archipelagos in this study, meets the pattern predicted by the SAR (Fig. 2.2). Vanuatu has approximately the proportion of the OMA fauna (Fig. 2.3a) and number of species (Fig. 2.5a) and endemic species (Fig. 2.5b) expected given the total archipelago area, and a greater proportion of this fauna than expected given the recent emergence history of this archipelago (Fig. 2.3b). Vanuatu has a lower proportion of the OMA diversity than would be expected given its distance from the faunal source (Fig. 2.3c) and degree of isolation (Fig. 2.3d). Total number of native species and endemic species in Vanuatu are higher than expected based on the size of the largest island in the archipelago (Figs. 2.4e,f), but lower than expected based on the maximum elevation of the archipelago (Figs. 2.4c,d).

Overall, these results do not support the suggestion that Vanuatu has a depauperate fauna. When the archipelagos were compared with respect to their ability to generate diversity through speciation as opposed to immigration, we found that Vanuatu has the expected rate of endemism (Fig. 2.4b). Furthermore, the ratio of both number of species and endemic species to the amount of time since emergence for Vanuatu is almost twice that for all other island groups considered in this study (Table 2.1). The development of high species richness over a short geologic timescale as seen in the Vanuatu Archipelago does not support the suggestion that the lizard fauna is depauperate. Rather, the lizard fauna of Vanuatu appears to fit the expectation for diversity relative to other OMA archipelagos.

It is important to note that our understanding of the reptile faunas of these archipelagos is still incomplete. Since 2000, 18 new species of lizards have been described from New Caledonia and two from the Solomon Islands (Appendix 1). The lizard fauna of Vanuatu has historically received less attention than most of the other island groups in this study; Vanuatu and Tonga are the only groups lacking a reptile field guide or monograph (Schwaner 1979, Bauer and Vindum

1990, Zug 1991, Bauer and Sadlier 1993, Gill 1993a, Bauer and Sadlier 1994, Bauer 1999, Bauer 2000, Bauer and Sadlier 2000, Morrison 2003, McCoy 2006). Recent collections in the Vanuatu archipelago and ongoing molecular work indicate that the actual diversity and endemism of the lizard fauna of Vanuatu is greater than currently described (Hamilton and Austin, unpublished data), providing even more support for the rejection of the historical characterization of the Vanuatu herpetofauna as depauperate.

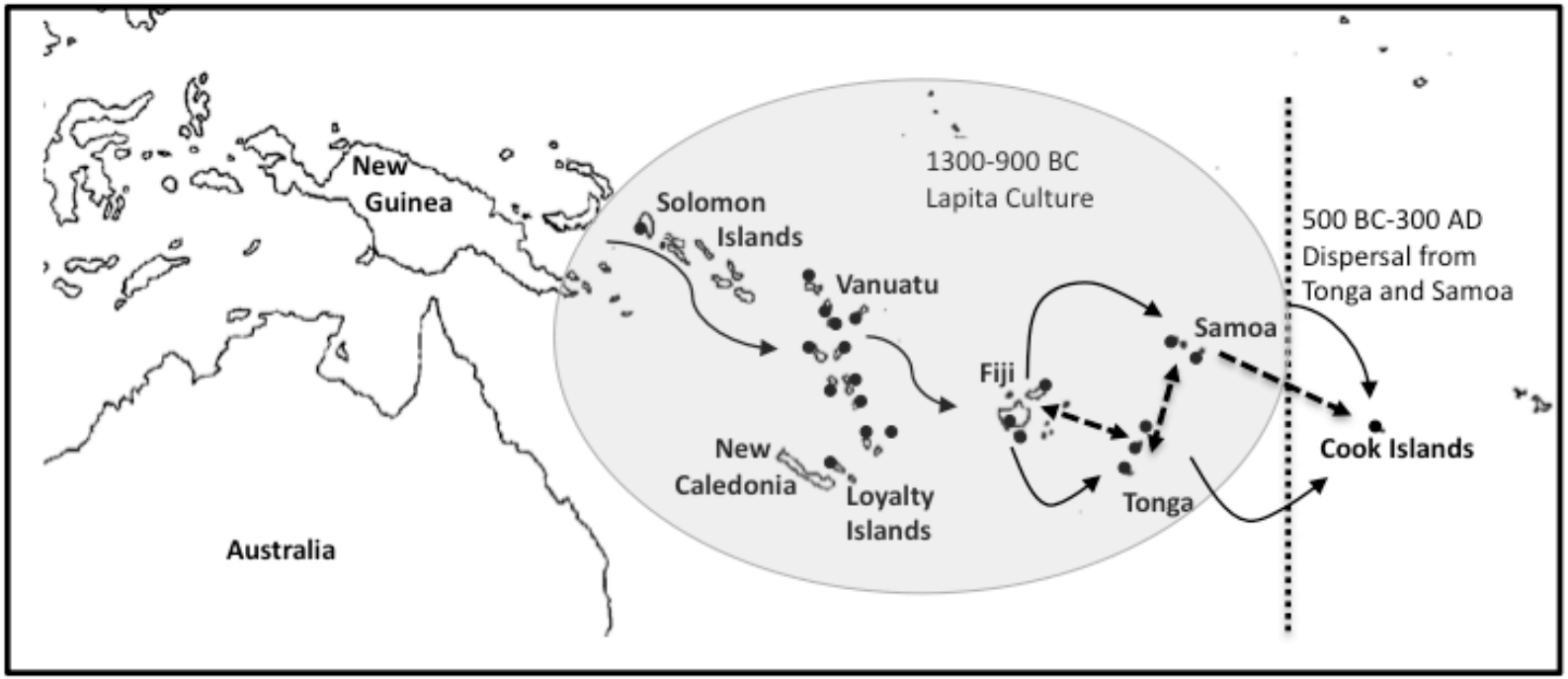
Does Choice of Island Groups Influence Perceptions of Diversity?

Inclusion or exclusion of archipelagos and island groups does influence the strength of the pattern recovered by the SAR (Fig. 2.5). Comparisons that contain multiple source faunas or islands with differing geologic origins confound the relationship between archipelago area, maximum elevation, and species richness and number of endemic species (Figs. 2.5a-d). Perhaps more importantly, choice of inclusion or exclusion of archipelagos based on their geologic history or the source of their lizard fauna altered the expected relationship between the number of species and endemic species in an island group and total archipelago area, maximum elevation, and size of the largest island, thus influencing perception of the diversity within each archipelago considered (Fig. 2.5). This perception bias may explain the historical perception that the Vanuatu Archipelago has a depauperate reptile fauna. The geographic proximity of Vanuatu to New Caledonia, an ancient continental landmass with a dissimilar, but species rich and highly endemic, fauna lends itself to a direct comparison of diversity between these two faunas, although the lack of a shared source fauna and the different geologic processes responsible for the formation of these islands renders such a comparison not valid.

CHAPTER 3: DISENTANGLING HISTORY IN OCEANIA: DIFFERENTIATING BETWEEN POLYNESIAN INTRODUCTIONS AND ENDEMIC SPECIES WITHIN THE LIZARD GENUS *EMOIA*

Research over the last several decades has highlighted the fact that the present day faunas of many insular systems, particularly those of Melanesia, Polynesia, and Micronesia, do not represent the true diversity resulting from evolutionary processes. Within the last 3500 years, humans have colonized the islands of the Pacific Ocean (Fig. 3.1), and massive extinctions and extirpation of island bird species resulted from land conversion for agriculture and predation by humans and the non-native mammals that accompanied these colonists (Steadman and Kirch 1990; Steadman 1993; Steadman 1995; Steadman et al. 1999). Early colonists brought plants and animals with them, both intentionally and as stowaways, and impact of these human-mediated introductions and extinctions has resulted in a modern Pacific Island fauna that is likely quite different from that present prior to human colonization. Extinctions on Pacific Islands resulted from four different types of human-influenced causes: (1) predation by humans on native fauna; (2) competition with (and predation on) the native fauna by plants and animals introduced by human colonists; (3) negative effects of parasites (such as Plasmodium) carried by introduced species on the native faunas; and (4) habitat loss and degradation due to habitat alteration and conversion for agriculture. The extent of the loss of diversity is dramatic, changing the present day distribution of many genera by eliminating the easternmost species in at least 18 bird taxa (Steadman 2006), and extinctions have occurred in all Pacific bird families (Steadman and Kirch 1990; Steadman 1993; Steadman 1995; Steadman et al. 1999). The reptile fauna has received less research attention, but similar patterns of extinction have occurred in Pacific Island reptile fauna (Pregill and Dye 1989; Pregill 1993; Pregill 1998; Pregill and Steadman 2000; Pregill and Worthy 2003; Pregill and Steadman 2004).

Figure 3.1. Map of the Pacific basin showing the regions of Melanesia and eastern Polynesia. The earliest settlers of this region, the extent of the Lapita culture is indicated in grey. Direction of human colonization of the Pacific are indicated with solid black arrows: the Lapita people had settled even the remote Melanesian Islands of Samoa and Tonga by 900 BC at the latest (Burley 1998; Kirch 2000). A second migration of people from the Lapita culture into the more remote Polynesian Islands (the region on the eastern side of the dotted line) began by 500 BC, with the Cook Islands and the Society Islands colonized first, likely prior to 300 AD (Rolett 1998). Documented trade routes are indicated with dashed arrows. Evidence from pottery shards so that Tonga served as a center of trade between Samoa and Fiji (Weisler and Woodhead 1995; Burley and Dickinson 2001). Evidence for trade between Samoa and the southern Cook Islands is based on basalt adzes (Weisler and Kirch 1996). Sample localities for individuals included in this study are indicated with black circles.


New Guinea
Solomon Islands
1300-900 BC
Lapita Culture
500 BC-300 AD
Dispersal from
Tonga and Samoa
Vanuatu
Samoa
Fiji
Cook Islands
New Caledonia
Loyalty Islands
Tonga
Australia

Pacific island faunal extinctions have received a large amount of attention (Steadman and Kirch 1990; Steadman 1993; Steadman et al. 2002a; Steadman et al. 2002b; Huynen et al. 2003; Gemmell et al. 2004; Baker et al. 2005; Steadman 2006; Boyer 2008) in part because these extinctions, if unrecognized, mask the true diversity of this important biodiversity hotspot. Incomplete distributional and diversity data can lead to erroneous inferences regarding the mechanisms of speciation that created the 'true' evolutionary history of these island systems, often referred to as the 'natural laboratory' for the fields of speciation, ecology, and evolution. Incomplete knowledge of human-mediated extinctions and the introduction of biota from outside of the Pacific, and thus the 'true' diversity of the Pacific Islands, is further compounded intra-Pacific introductions of native Pacific fauna and flora by early human colonists (Pregill and Steadman 2004; Lee et al. 2007; Keogh et al. 2008).

We examine how molecular data can be used to distinguish between human-mediated translocation of native faunas within Oceania and natural, waif overwater dispersal within the region (Fig. 3.2), and discuss the implications of disentangling population origin for our understanding of the evolution and maintenance of diversity in the islands of the Pacific Ocean. Distinguishing between populations whose distributions result from human movements from populations that dispersed by waif over-water dispersal or other natural means is difficult, but crucial, due to both the history of introductions in the Pacific and ongoing frequency of introductions in the present day. For example, unintentional introductions have resulted in 400,000 species having been introduced globally within the last 10,000 years (Pimentel 2001). Several criteria have been suggested for identification of introduced populations including: 1) knowledge of an introduction or recent arrival, 2) close association with humans or their habitats, places the species occurs, or 4) absence of subfossil remains from early archaeological sites (pre-human colonization) followed by increasing frequency in later, post-human colonization

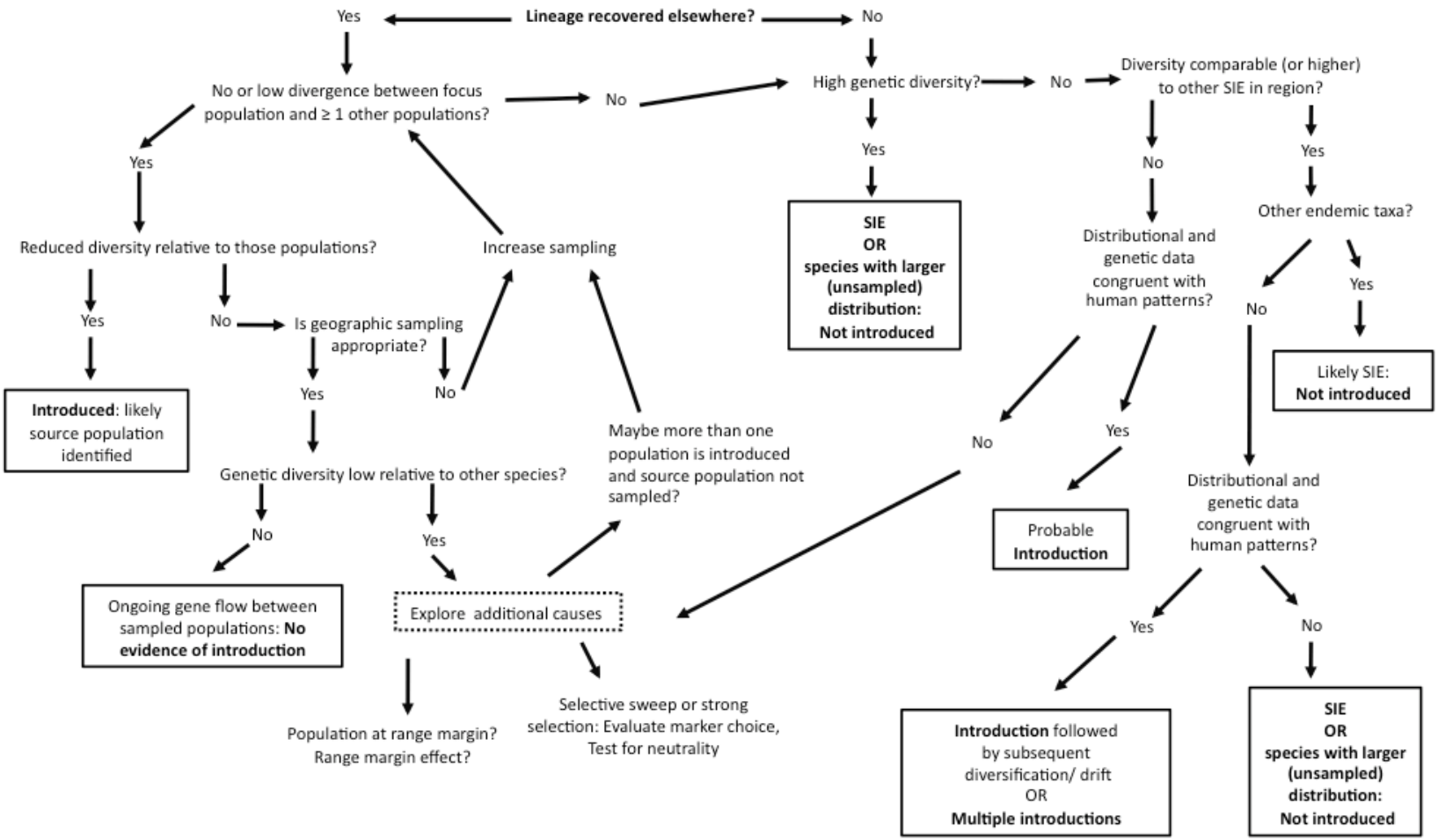


Figure 3.2. Conceptual framework for evaluating potential introductions. This decision tree incorporates phylogenetic hypotheses, population demographic data, and archaeological evidence and linguistic relationships to infer population history under a range of scenarios.

sites (Zug 1991; Weisler et al. 2006). Unfortunately, there are few studies of fossil and subfossil squamate remains on Pacific islands, and remains are difficult to locate and identify to the species-level (Pregill and Steadman 2000).

Molecular data have provided a useful tool for elucidating population history and even the likely source of identified introductions (Austin 1999c, a; Kolbe et al. 2004; Vences et al. 2004; Jesus et al. 2005; Rocha et al. 2005; Munoz-Fuentes et al. 2006; Kolbe et al. 2007). In some cases, however, the data are equivocal and could be interpreted as evidence for anthropogenic introductions, recent colonization via natural means, or a diversity-reducing event such as a population bottleneck (Fig. 3.2). Poor sampling or lack of knowledge of the range of a species may hamper investigators. Unraveling the history of introductions in the Pacific has been particularly difficult, in part because two distinct types of introductions have occurred since the arrival of humans in the region, each resulting in a different genetic signature. The introductions which have received the most research attention in the region are generally species introduced intentionally from outside of Oceania (such as pigs, chicken, dogs, and rats) because of the potential of the dispersal history of these Pacific populations to resolve questions about the human colonization of the Pacific (Matisoo-Smith et al. 1998; Matisoo-Smith and Robins 2004; Wilson and Lum 2006; Storey et al. 2007). Because these species originated from outside of the region, the introduced populations in the Pacific lack a genetic signature of regional diversification. For example, genetic data for *Rattus rattus* revealed a single mitochondrial haplotype with a Pacific basin-wide distribution (Matisoo-Smith et al. 1998).

In contrast to the generally intentional introduction of non-Pacific faunal elements, early humans in the Pacific also translocated native Pacific fauna, moving species around the Pacific as they colonized islands further eastward and traded with neighboring island groups. Some species were likely purposefully introduced due to their economic value or practical utility

(Pregill and Steadman 2004; Zerega et al. 2004; Clarke et al. 2006; Hinkle 2007; Lee et al. 2007; Keogh et al. 2008), whereas other introductions are presumed to have been the accidental result of stowaways on canoes, or in plant and animal cargo (Mortiz et al. 1993; Fisher 1997; Austin 1999b, c; Woodworth et al. 2005; Jarvi et al. 2008). As these species have a history of diversification within the Pacific Islands, we would expect to recover a signal of genetic diversity from populations which represent the native range of these species coupled with low, or no, genetic diversity from populations that represent introductions.

Molecular data have been used with varying degrees of success to resolve population history for Pacific lizards. *Gehyra oceanica*, a gecko species with a broad Pacific distribution, was found to be genetically variable throughout the region, with populations clustering congruent with geography, whereas a sympatric congener, *G. mutilata*, was found to be genetically uniform throughout the islands of the Pacific (Fisher 1997). These data suggest a human-mediated colonization history for *G. mutilata*, in contrast to natural dispersal for *G. oceanica* (Fisher 1997). The interpretation of the analysis of karyotype and mitochondrial DNA sequence data for three other gecko species with broad Pacific distributions (*Hemidactylus garnotti*, *H. frenatus*, and *Lepidodactylus lugubris*) were less clear (Moritz et al. 1993). Low genetic diversity and low sequence divergence among islands suggest a recent, rapid human-mediated introduction of *L. lugubris* and *H. garnotii* throughout the Pacific Islands, but a source population for these introductions could not be identified (Moritz et al. 1993). In contrast, and contrary to expectations, high genetic diversity and sequence divergence were recovered for *H. frenatus*, despite historical documentation of recent introductions of this species in the region, suggesting the geographic structure recovered was an artifact of sampling (Moritz et al. 1993). Mitochondrial DNA sequence data have also been used to elucidate the history of the skink *Lipinia noctua* in the Pacific basin. Populations sampled from Vanuatu, Fiji, and Polynesia were

extremely similar (mean divergence 0.008%) likely resulting from human-mediated dispersal, whereas *Lipina noctua* from Palau, New Guinea, the Solomon Islands, and Micronesia were genetically differentiated (mean divergence 9.7%), suggesting natural, pre-human dispersal (Austin 1999c, b).

The difficulty inherent in unraveling population history for lizards in the Pacific Islands is magnified and further confounded by their morphological conservatism (Austin 1995; Bruna et al. 1995; Bruna et al. 1996a). This conservatism has resulted in difficulties in resolving species boundaries, especially for Pacific skinks in the genus *Emoia* (Zug and Gill 1997; Austin and Zug 1999). We suggest that in many cases a multi-disciplinary approach is necessary to evaluate population history in this region, as a single approach will likely not apply to all putative introductions. Here, we present such an approach that incorporates information on distribution, phylogeny and novel statistical resampling techniques for comparing genetic diversity between native and hypothetically introduced species. As a case study, we evaluate a population of *Emoia* from the island of Rarotonga in the Cooks Islands that may have been introduced by humans. We place our examination of this population within a broader decision-tree framework for selecting methods of analysis and evaluating patterns of genetic variation that can be applied to test introduction hypotheses and distinguish true introductions from spurious inferences due to sampling bias.

MATERIALS AND METHODS

Species and Sampling

In the islands of Oceania, lizards in the genus *Emoia* represent an important component of the terrestrial vertebrate fauna, with multiple species occurring on most islands in the region. *Emoia* is species rich; the most recent review of the taxonomy, biogeography and morphology of the genus included 72 species (Brown 1991). Recent work indicates the true diversity of this genus

may be much greater, as morphological and molecular evolution may be uncoupled in Pacific skinks and new species of *Emoia* continue to be identified through ongoing collecting in the Pacific and molecular analysis of species with broad distributions (Bruna et al. 1995; Zug and Ineich 1995; Bruna et al. 1996a; Bruna et al. 1996b; Zug and Gill 1997; Zug and Ineich 1997).

One evolutionary lineage within *Emoia* contains 19 large-bodied, primarily arboreal species distributed in the islands of Oceania (Brown 1991). Species richness within this lineage is greatest in the Vanuatu Archipelago and the islands if Fiji (Hamilton et al. 2008b), and the lineage is distributed in the Solomon Islands, Vanuatu, the Loyalty Islands, Fiji, Samoa, and Tonga. Additionally, a population of *Emoia* has been reported from the island of Rarotonga in the Cooks Islands, and has historically been referred to as *E. trossula*. Recent phylogenetic analysis (Hamilton et al. unpublished data), however, does not support the validity of species status for *E. trossula*, and we refer to this population simply as '*Emoia* from Rarotonga' for the purpose of this paper. It has been suggested that the lizard fauna east of Samoa has been formed entirely due to human-mediated dispersal (Case, 1991; Crombie, 1988). Should this be the case, the Rarotonga population may have been introduced from elsewhere in the Pacific by humans either during initial colonization of the Pacific or via subsequent trading voyages among islands. Alternatively, it has been suggested that this population may be the sole member of the Cook Island lizard fauna to have dispersed via natural means (Crombie, 1988).

To distinguish between two alternative hypotheses regarding the dispersal and colonization of the Rarotonga population, we examine genetic variation from this population and from closely related individuals collected from adjacent island groups. As the genetic patterns that provide support for each hypothesis are different, analysis of this data may enable us to distinguish between natural dispersal and human-mediated introduction. Human-aided transport (and a relatively recent colonization event) would be supported by a lack of genetic

distinctiveness of the Rarotonga population, as well as low genetic diversity within this population. Should the Rarotonga population be genetically identical to another population, this would suggest a likely source. The natural dispersal hypothesis would be supported by an isolation by distance model of gene flow among populations in which more geographically distant populations are also more genetically distinct. Likewise, we would predict less diversification among geographically close populations under this hypothesis. Substantial genetic variation within the Rarotonga population or the genetic uniqueness of this population would also support the natural dispersal hypothesis.

Sequence Data Collection

As a first step, we used a well-resolved multi-locus phylogeny for this lineage of *Emoia* (Hamilton et al. unpublished data; Chapter 4 in this dissertation) to guide our choice of taxa for comparison to the Rarotonga population. Samples from 65 specimens representing 11 species of *Emoia* were included in this study (Table 3.1). DNA was isolated from either muscle or liver tissues using either a Qiagen DNA Extraction kit following manufacturer instructions, or using the standard method of proteinase K disgestion in lysis buffer followed by salt extraction (Aljanabi and Martinez 1997). We used three mitochondrial loci and one nuclear locus to ensure that a mix of relatively rapidly evolving and more slowly evolving gene regions were used to estimate phylogenetic relationships in this group.

We used PCR to amplify 1726 aligned bases of double-stranded mitochondrial DNA sequences (Cytb, Nd4, and CO1) and 289 aligned bases of nuclear DNA (*c-mos*) using the primers listed in Table 3.2. PCR was carried out in Omn-E or MJ PTC-200 thermal cyclers with the following conditions: (1) one cycle at 94°C for 2 min., 45 seconds at 48-56°C, and 72°C for either 1 min. or 1 min. and 20 seconds; (2) 34 cycles at 94°C for 2 min., 45 seconds at 48-56°C, and 72°C for either 1 min. or 1 min. and 20 seconds; (3) one cycle at 72°C for 6 min. A small

Table 3.1. Specimen data for this study. Acronyms for museum collections: CAS, California Academy of Sciences; LSUMZ, Louisiana State University Museum of Natural Science; USNM, United States National Museum. Acronyms for collector field numbers: CCA, Christopher C. Austin; ARB, Aaron R. Bauer; HBS, H. Bradley Shaefer.

Taxon	Locality	Museum or Collector Field No.
Emoia aneityumensis	Vanuatu	LSUMZ 89951-56, LSUMZ 89859-63, CCA 6415-16, 6420, 6441
Emoia concolor	Fiji: Taveuni	USNM 322523-25
Emoia concolor	Fiji: Beqa	USNM 333335, 333338, 333340
Emoia concolor	Fiji: Kadavu	USNM 333459-61
Emoia flavigularis	Solomon Islands	CCA 2701, 2716
Emoia mokosariniveikau	Fiji	USNM 322473
Emoia nigromarginata	Vanuatu	LSUMZ 89856-57
Emoia parkeri	Fiji	USNM 322681, 322474
Emoia samoensis	Samoa	ARB023334567, HBS 10907
Emoia samoensis	Samoa: Upolo	USNM 322754
Emoia samoensis	Fiji: Taveuni	USNM 322533-34, 499932-34, 499931, 332411-12
Emoia tongana	Samoa: Savaii	USNM 322458, 322748
Emoia tongana	Tonga	USNM 333673
Emoia tongana	Tonga: Haapi	USNM 333761-62
Emoia tongana	Tonga: Vavau	USNM 333672
Emoia concolor	Fiji: Viti Levu	USNM 333224
Emoia sp. nov.	Cook Islands	USNM 539182-86, 539190
Emoia sp. nov.	Tonga: Vava'u	USNM 333684
Emoia sp. nov.	Tonga: 'Eua	USNM 322228-30
Emoia sp. nov.	Tonga: Haapi	USNM 333763-64
Emoia sp. nov.	Vanuatu	CCA 6989, 7058, 6960

Table 3.2. Primers used in this study

Primer	Sequence (5' to 3')	Gene	Source
H 15149	AAA CTG CAG CCC CTC AGA ATG ATA TT	Cytb	Kocher et al. 1989
L 14841	AAA AAG CTT CCA TCC AAC ATC TCA GG	Cytb	Kocher et al. 1989
VR1 5	TAG ACT TCT GGG TGG CCA AAG AAT CA	CO1	Ivanova et al. 2006
VF1 5	TTC TCA ACC AAC CAC AAA GAC ATT GG	CO1	Ivanova et al. 2006
VF1i 5	TTC TCA ACC AAC CAI AAI GAI ATI GG	CO1	Ivanova et al. 2006
VR1d 5	TAG ACT TCT GGG TGG CCR AAR AAY CA	CO1	Ivanova et al. 2006
VR1i 5	TAG ACT6 TCT GGG TGI CCI AAI AAI CA	CO1	Ivanova et al. 2006
Nd4 F	CAC CTA TGA CTA CCA AAA GCT CAT GT	Nd4	Arevalo et al. 1994
Nd4 R	CAT TAC TTT TAC TTG GAT TTG CAC CA	Nd4	Arevalo et al. 1994
G73	GCG GTA AAG CAG GTG AAG AAA	*c-mos*	Saint et al. 1998
G74	TCA GCA TCC AAA GTC TCC ATT	*c-mos*	Saint et al. 1998
G77	TGG CYT GGT GCW NCA TNG ACT	*c-mos*	Saint et al. 1998
G78	AGR GTG ATR WCA AAN GAR TAR ATG TC	*c-mos*	Saint et al. 1998

number of samples were amplified under the following thermal cycler conditions: (1) one cycle at 94°C for 3 min. and 30 seconds, 50°C for 30 seconds, and 72°C for 1 min; (2) 44 cycles at 94°C for 30 seconds, 50°C for 30 seconds, and 72°C for 1 min.; (3) one cycle at 72°C for 10 min. Each 25 μl reaction contained 15.4 μl sterile water, 2.5 μl 10x PCR buffer, 1.5 μl of 25 nM $MgCl_2$, 0.5 μl of 10 nM dntp mix, 1 μl of 10 pM/ μl forward and reverse primers, 0.1 μl of Taq polymerase (Sigma-Aldrich, St. Louis, MO), and 3 μl of genomic DNA. All PCRS included a negative control (no DNA). Double-stranded PCR products were purified using the Ultra Clean Purification Kit (Mo Bio Laboratories, Solona Beach, CA) or ExoSAP-IT (USB Corporation, Cleveland, OH). PCR products were cycled sequenced using the original amplification primers and BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA). Sequenced products were cleaned up with CENTRI SEP Spin Columns and were visualized on an ABI 3100 sequencer. DNA sequences were edited with Sequencher 4.7, visually checked for accuracy, and aligned with Clustal X (Thompson et al. 1994).

We were unable to obtain good sequences for one or more gene segments for 8 of the 65 individuals sampled (4 of 11 species). In most cases only a single gene segment was not amplified (either *c-mos* or Nd4). We were able to amplify Cytb and CO1 for all individuals included in this study. We included individuals that were missing some data in this analysis as studies have shown that despite missing data, the phylogenetic information contained by data included for a taxon has utility in resolving relationships; inclusion of more individuals is more significant for obtaining phylogenetic accuracy than the potential negative effects of missing data (Wiens 2006; de Queiroz and Gatesy 2007).

Data Analysis

Phylogenetic Analysis

Phylogenetic trees were estimated using Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI). Paup* (4.10b) was used to reconstruct MP trees. Characters were equally weighted in heuristic searches using tree-bisection-reconnection branch swapping (to eliminate order biases), no upper bound for MaxTrees, the steepest descent option not in effect, and the MulTrees option selected. Clade support was evaluated by bootstrapping using 1000 pseudoreplicates and the same heuristic search conditions as described.

The GTR+I+G model was selected as the best fitting model of DNA substitution for the combined 2,015 bp dataset, using the Bayesian information criterion [BIC], which has been suggested as more appropriate than alternative criteria, as implemented in Modeltest v3.7 (Posada and Crandall 1998). Under this model, ML heuristic searches were conducted using the hill-climbing algorithm as implemented in the program GARLI v.0.96 (Zwickl 2006) with a random starting tree and default settings for the genetic algorithm. Identical topologies and nearly identical likelihood scores were obtained for five separate runs with GARLI, and 1,000 bootstrap pseudoreplicates were used to assess support for the resulting ML topology.

For BI, we first used the Akaike information criterion [AIC] in the program MrModelTest v.2.2 (Nylander et al. 2004) to select the best fitting model of DNA substitution for the dataset. MCMC analyses were run on the two different datasets with MrBayes 3.1 (Ronquist and Hulsenbeck 2003). The first dataset included 939 bp of mitochondrial data (Cytb and CO1) for all 65 individuals, whereas the second dataset included 1726 bp of mitochondrial data (Cytb, CO1, and Nd4) for 46 individuals. Two simultaneous independent runs of one cold and three heated MCMC chains, each with a different starting random tree, were conducted for 5 x 10^6 generations and trees were sampled every 1000 generations. To evaluate the consistency

of the results obtained from MrBayes, all analyses were run a second time. We examined potential scale reduction factors (PSRFs) and the standard deviation of split frequencies to determine that runs have converged on stationarity; PSRF values of 1.0 and an average standard deviation of split frequencies for both runs less than 0.01 indicated that both runs had converged on a stationary distribution. We used Tracer 1.4 (Rambaut and Drummond 2007) to examine tracer plots and determine if effective samples sizes were adequate (≥ 200) for estimates of the posterior distribution of tree likelihood and model parameters; results of this indicated that convergence had been reached and that the models had mixed well. For each independent run the first 2,000 trees were discarded as burn-in and a 50% majority-rule consensus tree was constructed from the remaining trees.

Comparison of Population-level Genetic Diversity Measures

To evaluate whether the genetic structure of the population of *Emoia* from Rarotonga, Cook Islands was congruent with the expected genetic diversity for a single island endemic, we compared measures of variation from the *Emoia* population on Rarotonga (n=6) to a closely related congeneric population known to be endemic to the island of Aneityum in the Vanuatu Archipelago (n=15), selected because of its similarity to Rarotonga in island area, elevation, and emergence history, all factors that may influence genetic diversity. We randomly selected six individual *E. aneityumensis* (to represent a sampling effort resulting in six individual, as we have for the Rarotonga population) using a bootstrap re-sampling approach with 1500 replicates. Replicates that did not select 6 different individuals were discarded, resulting in 485 datasets for *E. aneityumensis* comparable to the Rarotonga sample. This test is conservative, due to our exclusion of subsamples that did not include six unique individuals. Several diversity measures (π, θ_w, and haplotype diversity) were calculated for each of the 485 populations of *E.*

aneityumensis and the population from Rarotonga using Compute (Thornton 2003), and these diversity measures were compared between the two geographic locations.

As factors such as island size, habitat diversity, and island age (or length of population history) are likely to influence the genetic diversity within a population, we also considered the potential influence of these biotic and historical factors on the patterns of genetic variation recovered from the *Emoia* population on Rarotonga, Cooks Islands, and several closely related congeneric species from the nearby Vanuatu Archipelago (Table 3.3). We have chosen island endemics from the Vanuatu Archipelago for comparison with the Rarotonga *Emoia* because we have a much better knowledge of the distribution of species within Vanuatu as a result of our recent intensive research and collections in this group of islands. Measures of genetic diversity (π, θ_w, and haplotype diversity) from empirical data collected from seven populations including that on Rarotonga were regressed against total island size (km^2), maximum island elevation (which we are using as a rough proxy for habitat diversity as oceanic islands with little change in elevation are likely to have fewer habitats), and age of most recent, continual emergence for each island. We have chosen to use the length of time the island has been continually emergent as opposed to island age, as this is the measure of evolutionary time relevant to differentiation for populations of terrestrial organisms.

The relationship between the level of genetic diversity (as measured by π) and these biotic and historical characteristics of the island of Rarotonga was compared to the relationship between genetic diversity and these same island characteristics for 6 other species of *Emoia*, each endemic to a single island in within the Vanuatu Archipelago (Table 3.3). The purpose of this comparison was to evaluate the level of genetic diversity that we would expect to recover from closely related, single island endemic congeners in a neighboring archipelago from islands with different area, elevation, and length of time since emergence. We then compared the

Table 3.3. Lizards endemic to the Vanuatu Archipelago used in statistical resampling to generate datasets used for comparison with the population of *Emoia* on Rarotonga.

Taxon	**Museum No.**
Aneityum	
Emoia aneityumensis	LSUMZ 89951-56, LSUMZ 89859-63, CCA 6415-16, 6420, 6441
Ambae	
Emoia sp. nov.	CCA 6052-54, 6059-68, 6071
Erromango	
Emoia sp. nov.	CCA 6657, 6667-70, 6681-82
Ambrym	
Emoia sp. nov.	CCA 6960, 6989, 7058
Futuna	
Emoia erronan	LSUMZ 89958-67
Tanna	
Emoia sp. nov.	CCA 7202, 7209-11, 7223, 7231

diversity recovered from the Rarotonga population to these expected levels of diversity to evaluate whether the genetic diversity of the *Emoia* population from Rarotonga meets the expected pattern of genetic diversity for species of this lineage of *Emoia* that is endemic to a single island within Oceania. Should the genetic diversity for the Rarotonga population be lower than the level of genetic diversity recovered from these endemic *Emoia*, it would suggest that the Rarotonga population is not, in fact, a species endemic to the island of Rarotonga, but rather that it represents an introduction from elsewhere.

Archaeological Evidence and Linguistic Relationships

Based on archaeological data for Oceania, we developed a set of predictions for phylogenetic relationships and patterns of genetic diversity among island populations that would be congruent with a human-mediated dispersal history, and the relationships of native languages spoken throughout the region. If humans transferred *Emoia* among islands within the Pacific during initial colonization of the region, subsequent colonization of the eastern Pacific, or along trade routes we would expect to see the genetic signature of these movements reflected in the recovered phylogeny and population demographic structure.

The initial colonization of the Pacific by Austronesian speaking Lapita peoples occurred via the Solomon Islands, through Vanuatu and New Caledonia, and continuing eastward to the islands of Fiji, Tonga, and Samoa (Kirch and Green 1987; Kirch 1988, 2000; Burley and Dickinson 2001). This colonization history is concordant with the relationship among regional languages (Gray and Jordan 2001). As the Cook Islands were not colonized during the initial wave of human invasion into the Pacific, if Lapita peoples transported this lizard during the first stage of human colonization we would expect to recover evidence of this species on one or more of the islands involved in this initial migration in Oceania (i.e. the Solomon Islands, Vanuatu, New Caledonia, the Loyalty Islands, Fiji, Tonga, or Samoa). Expansion into the eastern Pacific,

including the Cook Islands, occurred from Tonga between 500 BC and 300 AD (Burley 1998; Burley and Dickinson 2001). Introduction of the *Emoia* population on Rarotonga during this wave of human movements would be suggested by a close relationship between the Rarotonga population and lizards from Tonga.

RESULTS

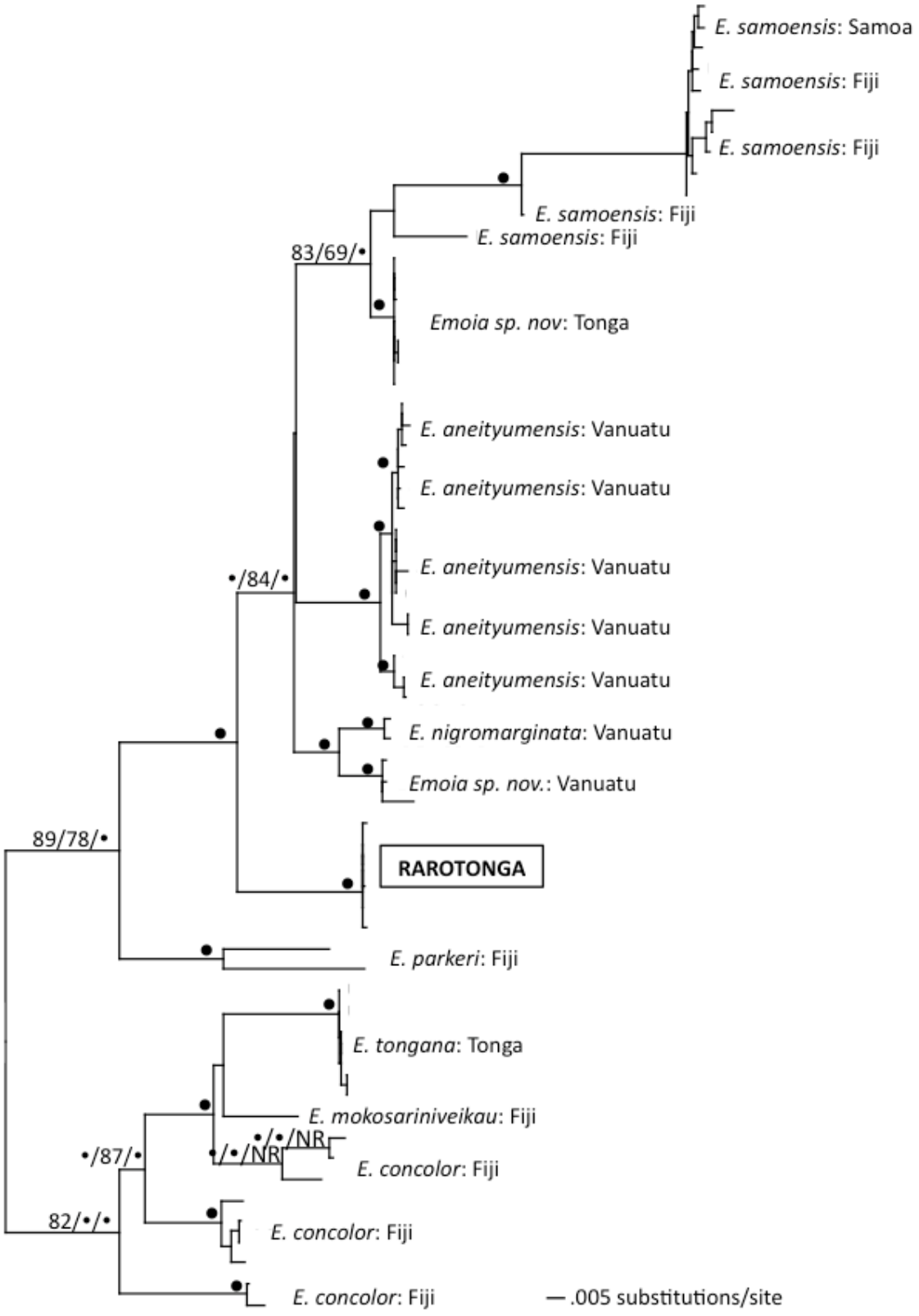
Tree Topology and Congruence Among Phylogenetic Methods

Reconstructed phylogenies inferred by MP, ML, and BI methods all had the same general topology, so only the ML tree is presented (Fig. 3.3) with support values generated using each method shown for each node in the topology. The six individuals from Rarotonga were recovered as a single, monophyletic clade, and the population is genetically distinct from all other species in the phylogeny. Despite the genetic distinctiveness of the individuals from Rarotonga (7% divergent from a species of *Emoia* endemic to Vanuatu and 10% divergent from *E. parkeri*, a species endemic to the Fijian archipelago), the amount of genetic diversity within this clade is low (<1%). The Rarotonga individuals are sister to a large clade containing populations of *Emoia samoensis* from Samoa and Fiji, a population of currently undescribed *Emoia* from Tonga, and three species endemic to the islands of the Vanuatu Archipelago (Fig. 3.3).

Comparison of Population-level Genetic Diversity Measures

The measure of π calculated from the empirical data for the Rarotonga population does not fall within the range of values of π generated for the datasets generated from the data for *E. aneityumensis* (Fig. 3.4). The value of π for the Rarotonga population is lower than π calculated from all 485 replicates generated from the *E. aneityumensis* data (Fig. 3.4a). The same result was recovered for estimates of θ_w (Fig. 3.4b); the value of θ_w for the Rarotonga population was lower than all θ_w values calculated for all 458 datasets generated from the *E. aneityumensis* data.

Figure 3.3. Maximum likelihood phylogeny using the GTR+I+G model of DNA substitution for a 2,015 bp dataset consisting of mitochondrial (Cytb, Nd4, and CO1) and nuclear (*c-mos*) DNA. Bootstrap values and posterior probabilities are shown for each node: ML (bootstrap values based on 1,000 pseudoreplicates) / MP (Bayesian posterior probabilities) / MP (bootstrap values based on 1000 pseudoreplicates). Support values ≥ 90% or 0.9 (•); nodes for which all three support measures are ≥ 90% or 0.9 are indicated with a single black dot (•). Nodes collapsed (i.e., the relationship among taxa was not resolved) in the MP topology are indicated with NR. Branch lengths are proportional to the number of substitutions per site (scale bar).


E. samoensis: Samoa
E. samoensis: Fiji
E. samoensis: Fiji
E. samoensis: Fiji
E. samoensis: Fiji
83/69/•
Emoia sp. nov: Tonga
E. aneityumensis: Vanuatu
E. aneityumensis: Vanuatu
•/84/•
E. aneityumensis: Vanuatu
E. aneityumensis: Vanuatu
E. aneityumensis: Vanuatu
E. nigromarginata: Vanuatu
Emoia sp. nov.: Vanuatu
89/78/•
RAROTONGA
E. parkeri: Fiji
E. tongana: Tonga
E. mokosariniveikau: Fiji
•/•/NR
•/87/•
•/•/NR
E. concolor: Fiji
82/•/•
E. concolor: Fiji
E. concolor: Fiji
— .005 substitutions/site

Haplotype diversity was also lower in the population from Rarotonga than from all replicates of the population of *E. aneityumensis* sampled from Aneityum, Vanuatu (Fig. 3.4c).

Relationship Between Genetic Diversity and Island Attributes

The *Emoia* population on Rarotonga had fewer haplotypes, lower haplotype diversity, and a lower value for k than all other populations examined for both CO1 and Nd4 (Table 3.4). A single CO1 haplotype and only two Nd4 haplotypes were recovered from the Rarotonga population (Table 3.4). Genetic diversity (π) for Nd4 of the Rarotonga population was lower than genetic diversity measured from all other species, and this reduced diversity is apparent when the relationships between genetic diversity (π) and several island characteristics are examined (Fig. 3.5). The Rarotonga population was also genetically uniform for the region of Cytb amplified (Table 3.4), although a single Cytb haplotype was also found in three other species. As for the Nd4 data, π estimated from Rarotonga was low compared to those for other species, even when viewed in light of island area, elevation, and emergence history (Fig. 3.5).

DISCUSSION

Differentiating between human-mediated dispersal and waif over-water dispersal is difficult, especially in light of the invasion of novel island systems by species native to other archipelagos in the Pacific following accidental or intentional translocation by Lapita people and early Polynesians. Although different population histories have unique predicted phylogenetic and population demographic signals, choosing between alternative predicted patterns and associated population history is not always possible. Our lack of knowledge of species' ranges, poorly resolved taxonomy and species boundaries, and inadequate sampling can often lead to an inability to differentiate among potential scenarios. This is especially problematic for tropical regions of the world, especially in the remote islands of the Pacific Ocean, where both the geographic distribution of sampling and often the numbers of individuals sampled are often

Figure 3.4. Genetic diversity measured by π, θ_w, and haplotype diversity for simulated populations of *E. aneityumensis*, a species endemic to the island of Aneityum in Vanuatu. Measures of π (A) θ_w (B), and haplotype diversity (C) generated by statistical resampling of *E. anietyumensis* for 458 datasets are illustrated by the bars of the histogram. The value for each diversity measure recovered from the empirical data for the *Emoia* population from Rarotonga is indicated with an arrow. For all three measures of population level genetic diversity Rarotonga has significantly lower diversity than all populations generated for Aneityum.

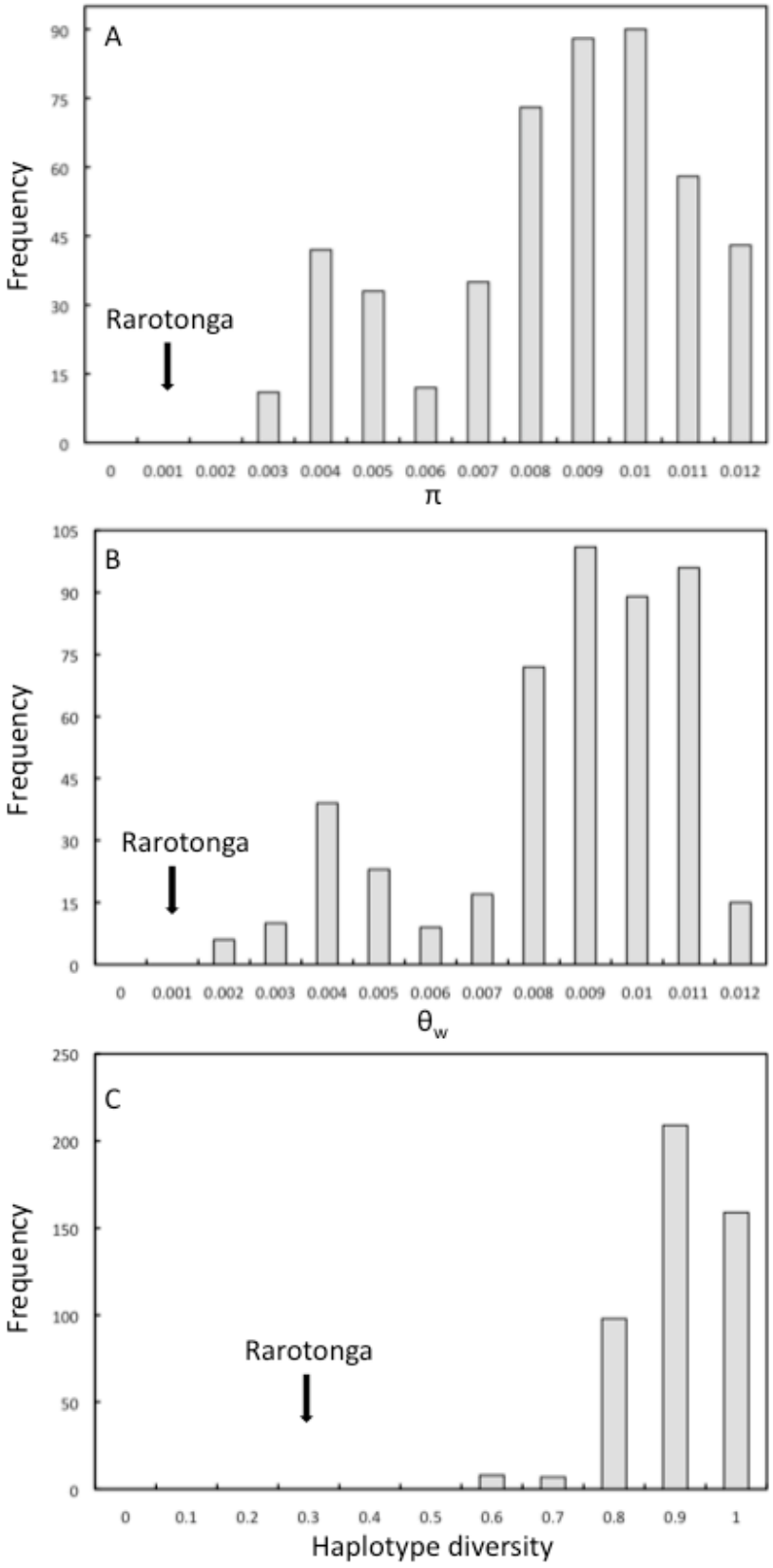

A
Frequency
Rarotonga
0 0.001 0.002 0.003 0.004 0.005 0.006 0.007 0.008 0.009 0.01 0.011 0.012
π
B
Frequency
Rarotonga
0 0.001 0.002 0.003 0.004 0.005 0.006 0.007 0.008 0.009 0.01 0.011 0.012
θw
C
Frequency
Rarotonga
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Haplotype diversity

Figure 3.5. Genetic diversity (π) for populations of *Emoia*, each endemic to a single island in the neighboring Vanuatu Archipelago. Genetic diversity (π) for each population is shown in relation several factors likely to influence genetic diversity: (A) island size, (B) island elevation, and (C) length of time the island has been emergent. Closed circles represent π calculated for Nd4 and open triangles represent π are calculated for Cytb. Genetic diversity (π) for the *Emoia* population on Rarotonga is circled.

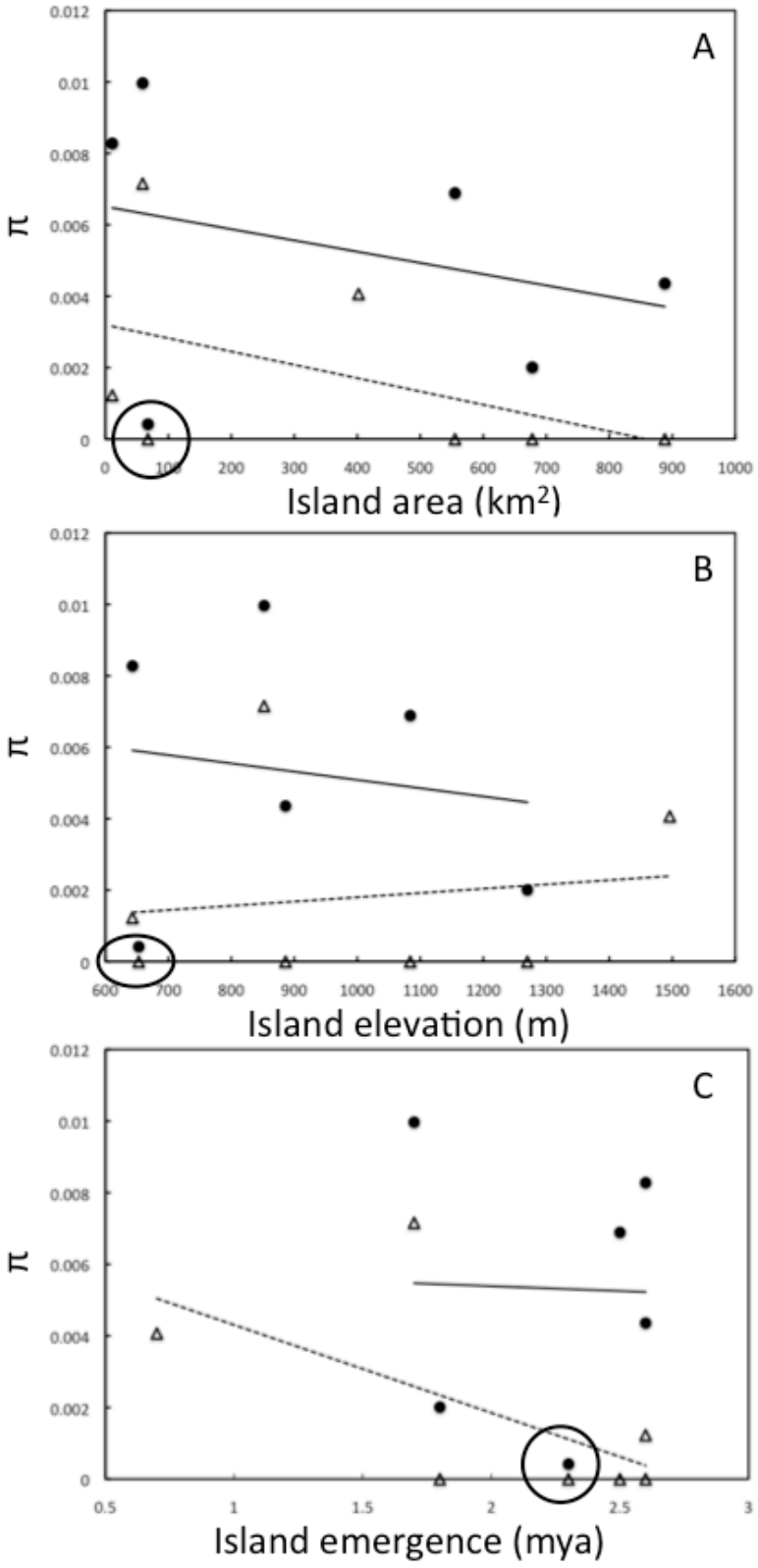

A
π
0.012
0.01
0.008
0.006
0.004
0.002
0
0
100
200
300
400
500
600
700
800
900
1000
Island area (km²)
B
π
0.012
0.01
0.008
0.006
0.004
0.002
0
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
Island elevation (m)
C
π
0.012
0.01
0.008
0.006
0.004
0.002
0
0.5
1
1.5
2
2.5
3
Island emergence (mya)

Table 3.4. Measures of population genetic variation calculated using DNAsp.

	N	Haps	HD	K	Variable sites	θ_w
CO1 (556bp)						
Aneityum	15	9	0.905	4.743	17	.009
Erromango	3	3	1.00	2.000	3	.004
Rarotonga	**6**	**1**	**0**		**0**	
Nd4 (765 bp)						
Ambrym	3	3	1.0	1.333	2	.002
Aneityum	7	5	0.905	7.801	17	.009
Erromango	3	3	1.0	3.333	5	.004
Futuna	3	3	1.0	6.333	9	.009
Rarotonga	**6**	**2**	**0.333**	**0.333**	**1**	**.001**
Tanna	15	7	0.867	2.362	9	.008
Cytb (330 bp)						
Ambae	16	3	.242	1.342	9	.008
Ambrym	3	1	0		0	
Aneityum	15	7	.867	2.362	9	.008
Erromango	9	1	0		0	
Futuna	18	3	0.386	0.405	2	.002
Rarotonga	**6**	**1**	**0**		**0**	
Tanna	6	1	0		0	

lacking as a result of the difficulties of adequately surveying small, isolated islands separated by large expanses of ocean. Inferences regarding population history must be viewed in light of the limits of the data that has been collected to avoid erroneous conclusions based on incomplete distributional data. By utilizing multiple approaches to data analysis and evaluating patterns of genetic variation, introduction hypotheses can be appropriately evaluated, distinguishing introductions from spurious inferences due to sampling bias.

The phylogenetic relationships among these species of *Emoia* provide support for both the human-mediated dispersal hypothesis and the possibility that the Rarotonga population dispersed by natural means and thus represents the sole species of reptile native to the Cook Islands. The population on Rarotonga forms a monophyletic group that is well differentiated (> 6% divergent from all other clades) from other species in the recovered topology (Fig. 3.3). Natural dispersal to Rarotonga would be supported by recovery of a monophyletic lineage that is genetically distinct from other species, the pattern for the data in our phylogeny. Natural dispersal would also be supported by a high amount of genetic diversity within the population from Rarotonga. In contrast, the topology of the phylogeny shows very low genetic variation (only 0.3%) within the clade from Rarotonga (Fig. 3.3), a pattern more consistent with a history of human-mediated dispersal.

The distinctiveness of the population of *Emoia* on Rarotonga coupled with such a low level of variation within the population is confusing, as the two sets of data do not support a single hypothesis but rather appear to contradict each other. There are two possible explanations for this pattern. The population of *Emoia* in the Cooks Island may represent a distinct, undescribed species that is endemic to Rarotonga and colonized Rarotonga through a natural dispersal event, not as a result of human influence. This possibility is supported by the high level of divergence between the Rarotonga population and other species in the phylogeny

(Fig. 3.3). An alternative explanation is that the Rarotonga population does represent a human-mediated introduction, as suggested by the low level of divergence within this clade. The source population, however, is not included in this phylogeny, resulting in the pattern of monophyly and high divergence from other species that we recovered for the *Emoia* population in Rarotonga (Fig. 3.3). The source population is not included in this phylogeny because the islands of the Pacific are poorly sampled. The *Emoia* population from Rarotonga represents a distinct, undescribed species in this second scenario as well; the native range of this species, and thus the origin of the introduction, remain unknown.

Comparison of population level genetic diversity measures for the Rarotonga population and the simulated populations of *E. aneityumensis* generated using a statistical resampling approach provide support for a human-mediated introduction to Rarotonga. In all 485 comparisons between equal-sized populations of *E. aneityumensis* (endemic to the island of Aneityum, Vanuatu) and empirical data from Rarotonga, three measures of genetic diversity (π, θ_w, and haplotype diversity) were greater for the population of *E. aneityumensis* in every case (Fig. 3.4). In addition, haplotype diversity was lower for the population from Rarotonga than populations of 6 single island endemic species of *Emoia* from Vanuatu for data from Cytb, Nd4, and CO1 (Table 3.5, Fig. 3.5). In combination, these results suggest that the amount of genetic diversity that we expect to observe in a species of this lineage of *Emoia* that is endemic to an oceanic island in the Pacific is much greater than the level of genetic variation present in the population from Rarotonga.

Relationship Between Genetic Diversity and Island Attributes

In contrast to expectations, we did not find a strong positive relationship between island area and genetic diversity (π) nor between π and the length of time an island has been emergent (Fig.

3.5a,c). Although not significant, the relationship between genetic diversity and island size and length of emergence was negative, suggesting that diversity may not increase over time, and may not be greater on larger islands. We caution, however, that the sample sizes of populations included in this comparison were very small, and were all closely related species, each endemic to a single island. Additionally, the differences among islands with respect to area were small (all islands in the comparison were <1000 km^2), and all islands in the comparison were formed as a result of same period of volcanic activity in the Vanuatu Arc (emergence times range from 0.5 mya to approximately 2.5 mya). There did not appear to be any relationship between island elevation and π (Fig. 3.5b). Islands in this comparison ranged in elevation from 650 m to 1500 m, although most islands had a maximum elevation of between 900 m and 1300 m. It is possible that π does not increase with an increase in habitat diversity, or that elevation was simply not an appropriate proxy for habitat diversity for these islands.

Archaeological Evidence and Linguistic Relationships

Relationships among Melanesian and Polynesian languages (Fig. 3.6) and the colonization route of the Pacific by Lapita peoples would lead to a predicted dispersal pathway from the Solomon Islands eastwards into the Vanuatu Archipelago, the Loyalty Islands, and New Caledonia, and then further eastwards in Fiji, Samoa and Tonga (Fig. 3.1). The topology that would be predicted by this introduction scenario is identical to the topology that would be predicted by a natural dispersal event from New Guinea or the Solomon Islands and eastward into the Pacific via a stepping stone dispersal pathway, as has been suggested for *Emoia* (Gibbons 1985; Brown and Gibbons 1986; Brown 1991). The topology we recovered does not provide evidence for a unidirectional colonization of the Pacific Islands from the Solomon Islands eastwards (Fig. 3.3). Although the Rarotonga population has a sister taxa relationship with a large clade containing species from Vanuatu, Fiji, Samoa, and Tonga, populations from

Table 3.5. Tests for human-mediated introduction as opposed to natural dispersal based on the decision tree outlines in Figure 3.2. Criteria used to evaluate the history of the *Emoia* population on Rarotonga, data presented in this study, and inferences suggested by these data.

Test	Result	Inference
Molecular phylogeny		
Population paraphyletic with respect to other population(s)	No	Unique lineage; lineage not recovered elsewhere
Genetic uniformity or low genetic variation within population	Yes	Introduced
Identical or similar to another population(s)	No	Not introduced
Statistical resampling		
π for Rarotonga relative to endemic congeners	Low	Introduced
θ_w for Rarotonga relative to endemic congeners	Low	Introduced
Haplotype diversity in Rarotonga relative to endemic congeners	Low	Introduced
Archaeological and linguistic data		
Congruence with introduction during initial colonization	No	Not introduced
Congruence with introduction during eastward expansion	Maybe	*No source population recovered?
Congruence with trade routes	Maybe	*No source population recovered?

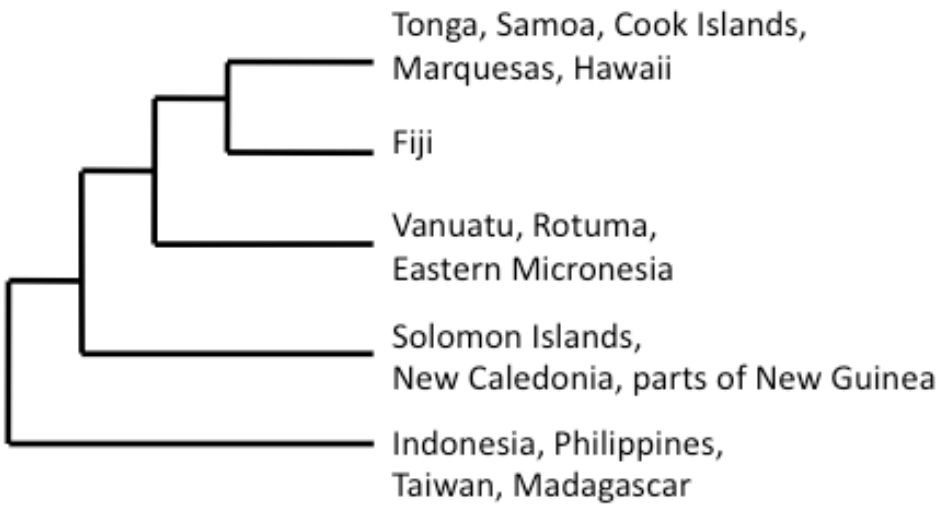


Figure 3.6. Relationships of languages spoken in Oceania (Kirch and Green, 1987).

other island groups fall out across multiple clades in the reconstructed phylogeny, suggesting a more complex pattern of dispersal and speciation.

Archaeological evidence suggests that Tonga served as a center for trade during this time, with trade routes established between Tonga and Samoa, Tonga and Fiji, Tonga and the Cook Islands, and even evidence for trade with Vanuatu (Kirch and Green 1987; Kirch et al. 1995; Burley 1998; Burley and Dickinson 2001). Direct trade between Samoa and the southern Cook Islands has also been inferred from the recovery of basalt adzes from prehistoric sites in the Cook Islands (Weisler and Woodhead 1995; Weisler and Kirch 1996). We suggest that this complex history of migrations and trade has likely resulted in the introduction of a species of *Emoia* to Rarotonga. As a result of the complexities of human history in Oceania, we cannot pinpoint a most likely origin for this introduction event. Due to both inter- and intra-archipelago voyaging of people throughout prehistory, Samoa, Fiji, and Tonga are all potential sources for the native range of the species that has been introduced to Rarotonga, Cook Islands. Given the difficulty inherent in effective sampling of Pacific Islands coupled with the relative paucity of research effort on the reptile fauna of these island groups, it is likely that the source population remains unsampled.

CHAPTER 4: ENDEMISM, MORPHOLOGICAL CONSERVATISM, AND EVIDENCE FOR ADAPTIVE DIVERSIFICATION IN A CLADE OF LIZARDS FROM OCEANIA

Much of the pioneering work on the processes that generate and maintain diversity has been performed in the islands of the tropical Pacific (Wallace 1858; Darwin 1859; Mayr 1942, 1965; Diamond 1974, 1977). Despite early interest in the Pacific island biotas, the evolutionary history of these biotas, and the extent of the diversity within them remain relatively unknown (Hamilton et al. 2008b). Predictions from island biogeography theory have been used to explain community composition (Gillespie et al. 1994; Willerslev et al. 2002; Gillespie et al. 2008; Hamilton et al. 2008b), however, less attention has been paid to how dispersal influences speciation over evolutionary time scales. The direction of dispersal is particularly controversial. Early researchers suggested that most dispersal proceeds from the mainland to islands (Mayr 1942; MacArthur and Wilson 1967), with the fauna of remote archipelagos resulting from *in situ* diversification or from multiple colonization events (Gillespie et al. 1994; Rundle and Nosil 2005). However, recent evidence suggests re-colonization of mainland areas by island fauna is more common than previously suspected (Filardi and Moyle 2005; Nicholson et al. 2005; Bellemain and Ricklefs 2008).

Remote archipelagos provide colonizers with unoccupied habitats, often with a reduced number of predators and competitors. Such conditions are ripe for adaptive radiation (MacArthur and Wilson 1967; Schluter 1988) resulting from selection on morphological and ecological traits associated with increasing specialization (Gillespie et al. 1994; Schluter 1996; Losos et al. 1998; Losos and Miles 2002). If populations adapt to divergent selection regimes, barriers to gene flow can result as a by-product of this divergent selection even in the absence of selective pressure on reproductive isolation itself (Schluter 2001; Rundle and Nosil 2005). Furthermore, adaptive divergence need not require geographic isolation (Endler 1977; Rice and

Hostert 1993; Niemiller et al. 2008), and divergence in the face of ongoing gene flow may be common (Nosil 2008). For archipelagos, this may be important when conspecific lineages repeatedly colonize an island, and resident, locally adapted lineages experience gene flow from more recent arrivals phenotypically distant from the local trait optima. The completion of reproductive isolation under this process would constitute allo-sympatric speciation (Coyne and Orr 2004). Alternately, sympatric speciation might occur on islands where diverse ecological opportunities exist. The possibility of sympatric speciation is supported by both theoretical (Kondrashov and Kondrashov 1999; Wilson et al. 2000; Bolnick and Fitzpatrick 2007; Gavrilets and Vose 2007) and recent empirical studies (Schliewen et al. 1994; Gislason et al. 1999; Savolainen et al. 2006). While rarely tested in island systems (Coyne and Price 2000), theoretical studies, laboratory experiments, and field data suggest a high degree of isolation from source biotas (i.e., habitats such as oceanic islands or volcanic crater lakes) and absence of predators and competitors (conditions that may occur on isolated islands) may promote sympatric speciation (Schliewen et al. 1994; Schluter 1996; Dieckmann and Doebeli 1999; Higashi et al. 1999; Kondrashov and Kondrashov 1999; Tregenza et al. 2000; Wilson et al. 2000) which may contribute to patterns of diversity on the remote islands of the Pacific Ocean. In general, much of the recent theoretical and empirical work has provided increasing evidence for the role of ecology in speciation (Funk 1998; Mizera and Meszéna 2003; Nosil et al. 2003; McKinnon et al. 2004; Nosil and Crespi 2006; Langerhans et al. 2007).

Changes in microhabitat use and invasion of novel environments occur concomitant with changes in morphology (Irschick et al. 1997; Losos et al. 1997; Losos et al. 1998; Losos and deQueiroz 1998)) and have been implicated in speciation in Hawaiian *Tetragnatha* spiders (Gillespie et al. 2008), and *Anolis* lizards (Losos et al. 1998). Such an adaptive response is due to strong selective pressure associated with resource utilization resulting in selection on

morphological traits (Kuo et al. 2007), often over very short timescales (Losos et al. 1997; Herrel et al. 2008), and directional selection is known to cause phenotypic diversification (Kingsolver et al. 2001; Rieseberg et al. 2002). Phenotypic divergence has broad implications for the diversification process, give that a positive relationship exists between ecological divergence (as measured by habitat, diet, and body size) and reproductive isolation across a broad range of taxa (Funk et al. 2006), further supporting the importance of ecology to speciation.

Lizards are an ideal system to examine how ecological factors influence speciation in Pacific island systems. First, lizards, especially skinks (Scincidae) and geckos (Gekkonidae) are frequently the most dominant terrestrial vertebrate lineage on remote Pacific oceanic islands (Hamilton et al. 2008b). Second, the link between morphology and ecology in lizards is well documented. For example, a strong association between morphological factors such as body shape or limb morphology and habitat use, degree of arboreality, and locomotion has been demonstrated in lizards (Losos 1989; Losos and Sinervo 1989; Losos 1990a; Miles 1994; Beuttell and Losos 1999; Melville and Swain 2000; Herrel et al. 2001; Kohlsdorf et al. 2001; Herrel et al. 2002; VanHooydonck et al. 2007; Kohlsdorf et al. 2008). Recent work has focused on the relationship between head size/shape and diet, bite force, gape size, and the ecological significance of these morphological characters to the feeding ecology, microhabitat use, and dietary breadth of lizards and other vertebrates (Wainwright 1988; Wainwright and Richard 1995; Verwaijen et al. 2002; Metzger and Herrel 2005; Herrel et al. 2007). Closely related species are generally thought to be able to co-exist through increased specialization for different components of the available resources (Hardin 1960; Chesson 1991; Tilmann 1994) and the need for specialization may be more pronounced on remote islands where resources may be less abundant than in mainland systems (MacArthur and Wilson 1963, 1967).

Although morphological variation may suggest adaptive diversification, relating variation to underlying genetic variation is required to rule out stochastic, selectively neutral explanations for observed patterns. Phylogenetic data can be used to test the influence of ecology on patterns of morphological variation (Thorpe et al. 1995; Thorpe 1996; Thorpe et al. 1996). A strong correlation between genetic distance and morphological variation would imply that nonadaptive phylogenetic effects have influenced morphological variation (Thorpe 1996). Alternatively, should the relationship between morphological and genetic variation be weak, adaptation to local ecological or environmental conditions may be generating the observed variation in morphology (Thorpe et al. 1995; Thorpe 1996; Thorpe et al. 1996; Thorpe and Stenson 2003; Thorpe et al. 2008). Combining information on morphology, ecology, and geographic distribution of the members of a species radiation with a robust hypothesis of the evolutionary relationships of the species in the group can permit an examination of both the spatial configuration of speciation, as well as the potential role of selection in the process of diversification in island systems.

We conduct such an analysis by inferring phylogenetic relationships among members of the *Emoia samoensis* group, a diverse radiation of skinks in the remote islands of the southwest Pacific (Fig. 4.1). We integrate this phylogenetic hypothesis with data on interspecific variation in fitness-related morphological traits to test hypotheses concerning the role of ecology in speciation and patterns of co-occurrence. Specifically, we address a series of related questions. (1) Is the *Emoia samoensis* group monophyletic? Monophyly of this species group would suggest a single invasion of the southwestern Pacific followed by subsequent speciation within Oceania. (2) Did colonization of the Pacific by the *Emoia samoensis* group occur in a unidirectional mainland to island direction?

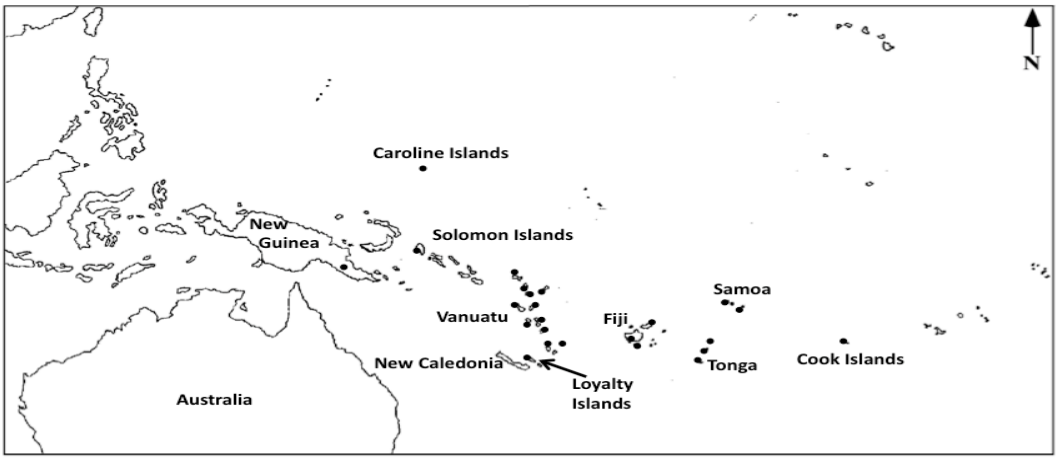


Figure 4.1. Collection localities (black circles) for species included in this study. Major island groups in Oceania are indicated.

Monophyly of each archipelago with *Emoia flavigularis* (Solomon Islands endemic) and perhaps *E. nigra* (distribution includes the Solomon Islands) as sister taxa to the remainder of the species group would support this dispersal pattern, as would reconstruction of *E. flavigularis* and *E. nigra* as the deeper branches in the phylogeny. (3) Do sister species have allopatric or sympatric distributions? Sympatric distributions for recently diverged taxa would suggest a mechanism other than gradual allopatric speciation or inter-island dispersal for speciation. Allopatric distributions would suggest the role of geographic separation in the speciation of this group. (4) Does morphological overlap occur between members of the *samoensis* group, and does the degree of overlap vary between sympatric and allopatric pairs? Increased morphological differentiation in ecologically significant traits between sympatric pairs would suggest mechanisms that might enable species to co-occur.

MATERIALS AND METHODS

Species and Sampling

In the islands of Oceania (Fig. 4.1), lizards in the genus *Emoia* represent an important component of the terrestrial vertebrate fauna, with multiple species occurring on most islands in the region. *Emoia* is species rich; the most recent review of the taxonomy, biogeography and morphology of the genus included 72 species (Brown 1991). Recent work indicates the true diversity of this genus may be much greater, as morphological and molecular evolution may be uncoupled in Pacific skinks and new species of *Emoia* continue to be identified through ongoing collecting in the Pacific and molecular analysis of species with broad distributions (Bruna et al. 1995; Zug and Ineich 1995; Bruna et al. 1996b; Bruna et al. 1996a; Zug and Gill 1997; Zug and Ineich 1997).

Brown (1991) subdivided *Emoia* into eight species groups, which he suggested represent distinct evolutionary lineages, based on morphology. One of lineages, the *samoensis* group, is restricted to the remote archipelagos of the southwest Pacific Ocean, and ranging from the

Solomon Islands southeastward to Vanuatu, the Loyalty Islands, Fiji, Tonga, and Samoa (Fig. 4.1). As described by Brown (1991), this group consists of thirteen species of primarily large-bodied, highly arboreal skinks, many of which have narrow distributions, endemic to a single remote archipelago or island.

The evolutionary relationships of these species have not been evaluated with morphological or molecular data, and a phylogeny for the *samoensis* group does not exist. Brown (1991) subdivided the *samoensis* group into two subgroups: the *samoensis* subgroup (*E. sanfordi, E. samoensis*, and *E. trossula*) and the *concolor* subgroup (which contains the remaining ten taxa). *Emoia mokosarinivekau* was described from a single specimen collected in Fiji and is thought to be a member of the *samoensis* group but its placement with respect to the two subgroups is uncertain (Zug and Ineich 1995). Additionally, our recent fieldwork in the Cook Islands, the Kingdom of Tonga, and the Vanuatu Archipelago have lead to the identification of several populations of *Emoia* which we suspect may represent new species in the *samoensis* group.

Samples from 56 specimens representing 29 species of *Emoia* and one outgroup taxon were included in this study (Table 4.1). To evaluate monophyly of the *Emoia samoensis* species group 17 non-*samoensis* group individuals, representing ten species and including members of all other seven putative species groups within *Emoia* (Brown 1991) were included. Thirteen of the 14 presently described species in the *samoensis* group were included in this study (Brown 1991; Zug and Ineich 1995); no tissues were available for *Emoia campbelli*, a species endemic to the Fijian archipelago and known only from the type locality (Zug 1991; Morrison 2003). We also included genetic material from six populations (collected by AMH or GRZ) that we suspected represented presently undescribed taxa within the *samoensis* group. Samples were chosen from the type locality whenever possible, and an attempt was made to include two

Table 4.1. Specimen data for samples used in this study. Acronyms: CAS, California Academy of Sciences; LSUMZ, Louisiana State University Museum of Natural Science; USNM, United States National Museum. Acronyms for field collection numbers: CCA, Christopher C. Austin; ARB, Aaron R. Bauer; HBS, H. Bradley Shaefer.

Taxon	Locality	Museum or Collector Field Id No.
Outgroup		
C. novahebredicus	Vanuatu	CCA 7713
Adspersa group		
Emoia adspersa	Samoa	USNM 322723
Atrocostata group		
Emoia atrocostata	Vanuatu	LSUMZ 89870-71
Baudini group		
Emoia loveredgei	PNG	CCA 1650
Emoia mivarti	PNG	CCA 1534
Cyanogaster group		
Emoia cyanogaster	Vanuatu	LSUMZ 89990-91
Cyanura group		
Emoia caeruleocauda	Vanuatu	CCA 7183, 7204
Emoia cyanura	Vanuatu	CCA 7405, 7430, 7343
Emoia impar	Vanuatu	CCA 7434
Physicae group		
Emoia physicae	PNG	CCA 0002
Emoia popei	PNG	CCA 0003
Ponapea group		
Emoia ponapea	Ponapei	CCA 1141-42
Samoensis group		
Emoia aneityumensis	Vanuatu	LSUMZ 89952-53
Emoia concolor	Fiji: Taveuni	USNM 322525, 333335
Emoia erronan	Vanuatu	LSUMZ 89958, CCA 7420
Emoia flavigularis	Solomon Isl.	CCA 2701-2716
Emoia loyaltiensis	Loyalty Isl.	CAS 229386-87
Emoia mokosariniveikau	Fiji	USNM 322473
Emoia nigra	Vanuatu	CCA 6084, 6135, 2715
Emoia nigromarginata	Vanuatu	LSUMZ 89856-57
Emoia parkeri	Fiji	USNM 322681, 322474
Emoia samoensis	Fiji: Taveuni	USNM 499933-34
Emoia samoensis	Samoa	ARB023334567, HBS 10907
Emoia sanfordi	Vanuatu	LSUMZ 90890, 90892
Emoia sp. nov.	Tonga: Vava'u	USNM 333684
Emoia sp. nov.	Tonga: 'Eua	USNM 322228
Emoia sp. nov.	Cook Isl.	USNM 539182, 539185
Emoia sp. nov.	Vanuatu	CCA 6026, 6071
Emoia sp. nov.	Vanuatu	CCA 6668, 6669
Emoia sp. nov.	Vanuatu	CCA 6989, 7058
Emoia sp. nov.	Vanuatu	USNM 334291, CCA 7209
Emoia tongana	Tonga	USNM 333761, USNM 333673

individuals from each species in the analysis. The inclusion of multiple individuals from each species also assists with sequence alignment and confirms sequence identity. *Cryptoblepharus* has been suggested to be closely related to, but distinct from, *Emoia* (Smith et al. 2007), so *Cryptoblepharus novahebredicus* was chosen for use as an outgroup.

Sequence Data Collection

DNA was isolated from either muscle or liver tissues using either a Qiagen DNA Extraction kit following manufacturer instructions, or using the standard method of proteinase K digestion in lysis buffer followed by salt extraction (Aljanabi and Martinez 1997). We used three mitochondrial loci and one nuclear locus to ensure that a mix of relatively rapidly evolving and more slowly evolving gene regions were used to estimate phylogenetic relationships in this group.

We used PCR to amplify 1737 aligned bases of double-stranded mitochondrial DNA products (Cytb, Nd4, and CO1) and 417 aligned bases of double-stranded nuclear DNA (*c-mos*) products using the primers listed in Table 4.2. PCR was carried out in Omn-E or MJ PTC-200 thermal cyclers with the following conditions: (1) one cycle at 94°C for 2 min., 45 seconds at 48-56°C, and 72°C for either 1 min. or 1 min. and 20 seconds; (2) 34 cycles at 94°C for 2 min., 45 seconds at 48-56°C, and 72°C for either 1 min. or 1 min. and 20 seconds; (3) one cycle at 72°C for 6 min. A small number of samples were amplified under the following thermal cycler conditions: (1) one cycle at 94°C for 3 min. and 30 seconds, 50°C for 30 seconds, and 72°C for 1 min; (2) 44 cycles at 94°C for 30 seconds, 50°C for 30 seconds, and 72°C for 1 min.; (3) one cycle at 72°C for 10 min. Each 25 μl reaction contained 15.4 μl sterile water, 2.5 μl 10x PCR buffer, 1.5 μl of 25 nM $MgCl_2$, 0.5 μl of 10 nM dntp mix, 1 μl of 10 pM/ μl forward and reverse primers, 0.1 μl of Taq polymerase (Sigma-Aldrich, St. Louis, MO), and 3 μl of genomic DNA.

Table 4.2. Primers used in this study.

Primer	Sequence (5' to 3')	Gene	Source
H 15149	AAA CTG CAG CCC CTC AGA ATG ATA TT	Cytb	Kocher et al. 1989
L 14841	AAA AAG CTT CCA TCC AAC ATC TCA GG	Cytb	Kocher et al. 1989
VR1 5	TAG ACT TCT GGG TGG CCA AAG AAT CA	CO1	Ivanova et al. 2006
VF1 5	TTC TCA ACC AAC CAC AAA GAC ATT GG	CO1	Ivanova et al. 2006
VF1i 5	TTC TCA ACC AAC CAI AAI GAI ATI GG	CO1	Ivanova et al. 2006
VR1d 5	TAG ACT TCT GGG TGG CCR AAR AAY CA	CO1	Ivanova et al. 2006
VR1i 5	TAG ACT6 TCT GGG TGI CCI AAI AAI CA	CO1	Ivanova et al. 2006
Nd4 F	CAC CTA TGA CTA CCA AAA GCT CAT GT	Nd4	Arevalo et al. 1994
Nd4 R	CAT TAC TTT TAC TTG GAT TTG CAC CA	Nd4	Arevalo et al. 1994
G73	GCG GTA AAG CAG GTG AAG AAA	*c-mos*	Saint et al. 1998
G74	TCA GCA TCC AAA GTC TCC ATT	*c-mos*	Saint et al. 1998
G77	TGG CYT GGT GCW NCA TNG ACT	*c-mos*	Saint et al. 1998
G78	AGR GTG ATR WCA AAN GAR TAR ATG TC	*c-mos*	Saint et al. 1998

All PCRs included a negative control (no DNA). Double-stranded PCR products were purified using the Ultra Clean Purification Kit (Mo Bio Laboratories, Solona Beach, CA) or ExoSAP-IT (USB Corporation, Cleveland, OH). PCR products were cycle sequenced using the original amplification primers and BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA). Sequenced products were cleaned up with CENTRI SEP Spin Columns and were visualized on an ABI 3100 sequencer. DNA sequences were edited with Sequencher 4.7, visually checked for accuracy, and aligned with Clustal X (Thompson et al. 1994).

We were unable to obtain good sequences for one or more gene segments for 11 of the 56 individuals sampled (2 of 18 presumptive species from the *Emoia samoensis* group and 6 of 11 species of *Emoia* from other lineages). In almost all cases only a single gene segment was not amplified (either *c-mos*, Nd4, or Cytb); for one *E. nigra* we could not amplify either Cytb or Nd4. We were able to amplify CO1 for all individuals included in this study. We included individuals that were missing some data in this analysis as studies have shown that despite missing data, the phylogenetic information contained by data included for a taxon has utility in resolving relationships; inclusion of more individuals is more important for obtaining phylogenetic accuracy than the potential negative effects of missing data (Wiens 2006; de Queiroz and Gatesy 2007).

Phylogenetic Analysis

Phylogenetic trees were estimated using Maximum Parsimony (MP), Maximum likelihood (ML), and Bayesian Inference (BI). Paup* (version) was used to reconstruct MP trees. Characters were equally weighted in heuristic searches using 1,000 random stepwise additions (with one tree held at each step during stepwise addition) tree-bisection-reconnection branch swapping (to eliminate order biases), no upper bound for MaxTrees, the steepest descent option not in effect, and the MulTrees option selected. Clade support was evaluated by bootstrapping using 500

pseudoreplicates and the same heuristic search conditions as described above but using only 100 random stepwise additions.

Maximum Likelihood

The GTR+I+G model was selected as the best fitting model of DNA substitution for the combined 2,154 bp dataset, using the Akaike information criterion [AIC] as implemented in Modeltest v3.7 (Posada and Crandall 1998). Under this model, ML heuristic searches were conducted using the hill-climbing algorithm as implemented in the program GARLI v.0.96 (Zwickl 2006) with a random starting tree and default settings for the genetic algorithm. Identical topologies and likelihood scores were obtained for five separate runs with GARLI, and 1,000 bootstrap pseudoreplicates were used to assess support for the resulting ML topology.

Bayesian Inference

For BI, we first used the AIC in the program MrModelTest v.2.2 (Nylander et al. 2004) to select the best fitting model of DNA substitution for the dataset. MCMC analyses were run on both partitioned and unpartitioned datasets (Table 4.3) with MrBayes 3.1 (Ronquist and Hulsenbeck 2003). Two simultaneous independent runs of one cold and three heated MCMC chains, each with a different starting random tree, were conducted for 5×10^6 generations and trees were sampled every 100 generations. To evaluate the consistency of the results obtained from MrBayes, all analyses were repeated. We examined potential scale reduction factors (PSRFs) and the standard deviation of split frequencies to determine that runs converged on stationarity; PSRF values of 1.0 and an average standard deviation of split frequencies for both runs less than 0.01 indicated that both runs had likely converged on a stationary distribution. We used Tracer 1.4 (Rambaut and Drummond 2007) to examine tracer plots and determine if effective sample sizes were adequate ($\geq$ 200) for estimates of the posterior distribution of tree

Table 4.3. Summary of initial model parameters used in Bayesian analyses.

Partition	Model	-ln*L*	AIC	Base frequencies		Rate Matrix		
Cytb	HKY+I+G	3294.390	6600.780	A = 0.3121	C = 0.3343	Ti/Tv Ratio = 5.6149		
				G = 0.1128	T = 0.2408			
c-mos	HKY+I+G	1257.973	2527.947	A = 0.3019	C = 0.1755	Ti/Tv Ratio = 1.7682		
				G = 0.2384	T = 0.2842			
Nd4	GTR+I+G	8072.752	16165.504	A = 0.3522	C = 0.3459	A-C = 0.4861	A-G = 7.7893	A-T = 0.3881
				G = 0.0745	T = 0.2275	C-G = 0.3337	C-T = 4.5324	G-T = 1.0000
CO1	GTR+I+G	6364.785	12749.569	A = 0.2630	C = 0.3110	A-C = 1.1056	A-G = 18.2264	A-T = 1.9122
				G = 0.1589	T = 0.2671	C-G = 0.4359	C-T = 9.5634	G-T = 1.0000
MtDNA	GTR+I+G	18589.631	37199.2617	A = 0.3151	C = 0.3312	A-C = 0.7966	A-G = 9.4511	A-T = 0.8648
				G = 0.1121	T = 0.2416	C-G = 0.3838	C-T = 7.0767	G-T = 1.0000
All	GTR+I+G	20621.996	41263.992	A = 0.3201	C = 0.3056	A-C = 0.8453	A-G = 7.7404	A-T = 0.8421
				G = 0.1265	T = 0.2478	C-G = 0.3739	C-T = 6.4970	G-T = 1.0000

likelihood and model parameters; results of this indicated that convergence had been reached and that the models had mixed well. For each independent run the first 6,000 trees were discarded as burn-in, as in both cases convergence had occurred, and a 50% majority-rule consensus tree was constructed from the remaining 88,002 trees.

Morphological Data Collection and Analysis

Measurements and Choice of Specimens

90 specimens, representing all 19 species in the *samoensis* species group, were measured for morphological characters suggested to be ecologically relevant (Table 4.4). Body size dimensions are strongly selected in arboreal lizards (Malhotra and Thorpe 1997; Losos et al. 1998), and morphological characters such as snout-vent length (SVL) and hindlimb length have been closely linked to habitat use (Moermond 1979; Losos 1990b; Losos et al. 1998). Eleven morphological characters were measured: SVL, trunk length, hindlimb length, snout-forelimb length, head length, jaw width, head height, distance from the snout to eye, distance from nares to eye, snout width, and the inter-orbital distance. Measurements were taken to the nearest 0.01mm using digital calipers. We chose traits likely to have fitness consequences because locomotion is ecologically important, enabling lizards to escape from predators and to find food or mates (Huey and Stevenson 1979; Arnold 1983; Losos 1990b; Garland 1994). Additionally, larger head size has been shown to increase gape width and bite force in lizards (Herrel et al. 2001; Herrel et al. 2003; Meyers et al. 2004; McBrayer et al. 2005; Brecko et al. 2008). Gape width and bite force are ecologically important because they increase the food resources available by enabling capture of both larger and harder prey items (Herrel et al. 2006).
When possible, individuals used in reconstructing the phylogenetic hypothesis were measured for morphological data, and a few additional adult individuals from the same geographic areas

represented in the molecular data were included to increase sample size (Table 4.4). In a few cases individuals included in the phylogenetic reconstruction were either juveniles, were not available for morphological measurements, or were in poor condition. In these cases (*E. loyaltiensis*, *Emoia* E, *E. parkeri*, *E. campbelli*, and *E. nigra*), we collected morphological data from individuals collected from the same locality, and in some cases at the same time as, the individuals included in our molecular analysis. Although the phylogeny includes three *E. nigra* individuals, only the two *E. nigra* from Vanuatu were included in our genetic distance matrix; likewise, only *E. nigra* from Vanuatu were included in our morphological data collection. Measurements were made by either GRZ or AMH and a separate correction factor was applied to each trait to adjust for inter-researcher measurement variation for that trait.

Mantel Matrix Regressions

To quantify morphological variation among species, we performed a principle components analysis (PCA) on the morphological data with SPSS (v.15) to estimate size (PC1) and shape (PC2) metrics. To test the hypothesis that interspecific morphological variation is significantly correlated with phylogeny (and thus more likely due to genetic drift), we performed Mantel matrix regressions of morphological distance on genetic distance. Specifically, we first computed separate Euclidean distance matrices for each principle component on the mean taxon principle component scores.

For our genetic predictor matrix, we then calculated patristic distances based on the ML multi-locus phylogeny with the program PATRISTICv1.0 (Fourment and Gibbs 2006). Mean pairwise genetic distances were computed for each species-pair comparison, from which genetic distance matrices were constructed. We performed Mantel matrix regressions with Isolation By Distance Web Service v3.15 (Jensen et al. 2005; Bohonak 2002) to examine the relationship

Table 4.4. Specimens examined for morphological component of this study. Acronyms: CAS, California Academy of Sciences; LSUMZ, Louisiana State University Museum of Natural Science; USNM, United States National Museum. Acronyms for field collection numbers: CCA, Christopher C. Austin; AMH, Alison M. Hamilton.

Taxon	**Locality**	**Museum and Collector Field Nos.**
Emoia aneityumensis	Vanuatu	CCA 6417, CCA 6427, CCA 6429, CCA 6414, CCA 6401, CCA 6409
Emoia campbelli		CAS155973, CAS155967
Emoia concolor	Fiji: Taveuni	USNM322525
Emoia concolor		USNM322524, USNM333340, USNM322521, USNM322671
Emoia erronan	Vanuatu	CCA6455, CCA6488, CCA7423, CCA6459, CCA6460, CCA6471, CCA7412, CCA7420, CCA7456, CCA7472
Emoia flavigularis	Solomon Isl.	CCA2701, CCA2716
Emoia loyaltiensis	Loyalty Isl.	AMNH60460
Emoia mokosariniveikau	Fiji	USNM322473
Emoia nigra	Vanuatu	AMH013, AMH038, AMH087, CCA6035, CCA6566, CCA7656, CCA7677, CCA7690, CCA6106, CCA7622, CCA7678
Emoia nigromarginata	Vanuatu	CCA6324, CCA6326
Emoia parkeri	Fiji	CAS147570, CAS156005, CAS147572
Emoia samoensis		USNM499934
Emoia sanfordi	Vanuatu	AMH209, CCA6162, CCA6164, CCA7605, CCA7581, CCA6160
Emoia 'A'	Vanuatu	CCA6014, CCA6052, CCA6043, CCA6057, CCA6063, CCA6067, CCA6053, CCA6071, CCA6564, CCA6572, CCA6026, CCA6032, CCA6062
Emoia 'B'	Vanuatu	CCA6960, CCA7058
Emoia 'C'	Tonga	USNM333684, USNM259332, USNM259331
Emoia 'D'	Cook Isl.	USNM539181, USNM539183, USNM533721, USNM539182
Emoia 'E'	Vanuatu	CCA7211, CCA7223
Emoia 'F'	Vanuatu	CCA6718, CCA6703, CCA6681, CCA6670, CCA6682, CCA6669, CCA6668, CCA6657, CCA6690, CCA6689
Emoia tongana	Tonga	CAS176465, CAS176464, CAS172208, CAS176440, CAS176463

between morphological distance and genetic distance by regressing the principal component score matrix (morphology) on the genetic distance matrix. We examined the relationships resulting from this regression to address the role of adaptation in driving morphological diversification. We tested the expectation that morphological divergence would be greater in taxa with spatial overlap by using t-tests on distance matrix values from sympatric and allopatric species pairs.

RESULTS

Tree Topology and Congruence Among Phylogenetic Methods

Reconstructed phylogenies inferred by MP, ML, and BI methods all had the same general topology (Fig. 4.2). Topologies recovered with ML and BI were identical; comparisons between these two methods of construction reveal only slight variation in the level of support for some nodes in the phylogeny. *Emoia flavigularis* is recovered as the sister taxa to all other members of the *E. samoensis* group, which is strongly supported as a monophyletic clade in topologies recovered by all three phylogenetic methods (Fig. 4.2). The MP topology was largely congruent with the topologies recovered using ML and BI methods, with one exception. MP methods recovered a poorly supported node including *E. nigra* as the sister taxon to a clade containing all the remaining *E. samoensis* group species except *E. flavigularis*, but this relationship was not recovered with ML and BI methods. Instead, ML and BI methods place *E. nigra* as sister to a smaller clade consisting of *E. sanfordi* (endemic to the Vanuatu archipelago) and *E. loyaltiensis* (endemic to the Loyalty Islands), within a clade that also contains an additional taxon endemic to Vanuatu (Fig. 4.2). Additionally, MP analysis produced a polytomy for the relationship of the *ponapea* group with respect to the *cyanogaster* species group and a clade containing the members of the *atrocostata*, *adspersa*, *baudini* and *physicae* species groups.

Relationships Within *Emoia*

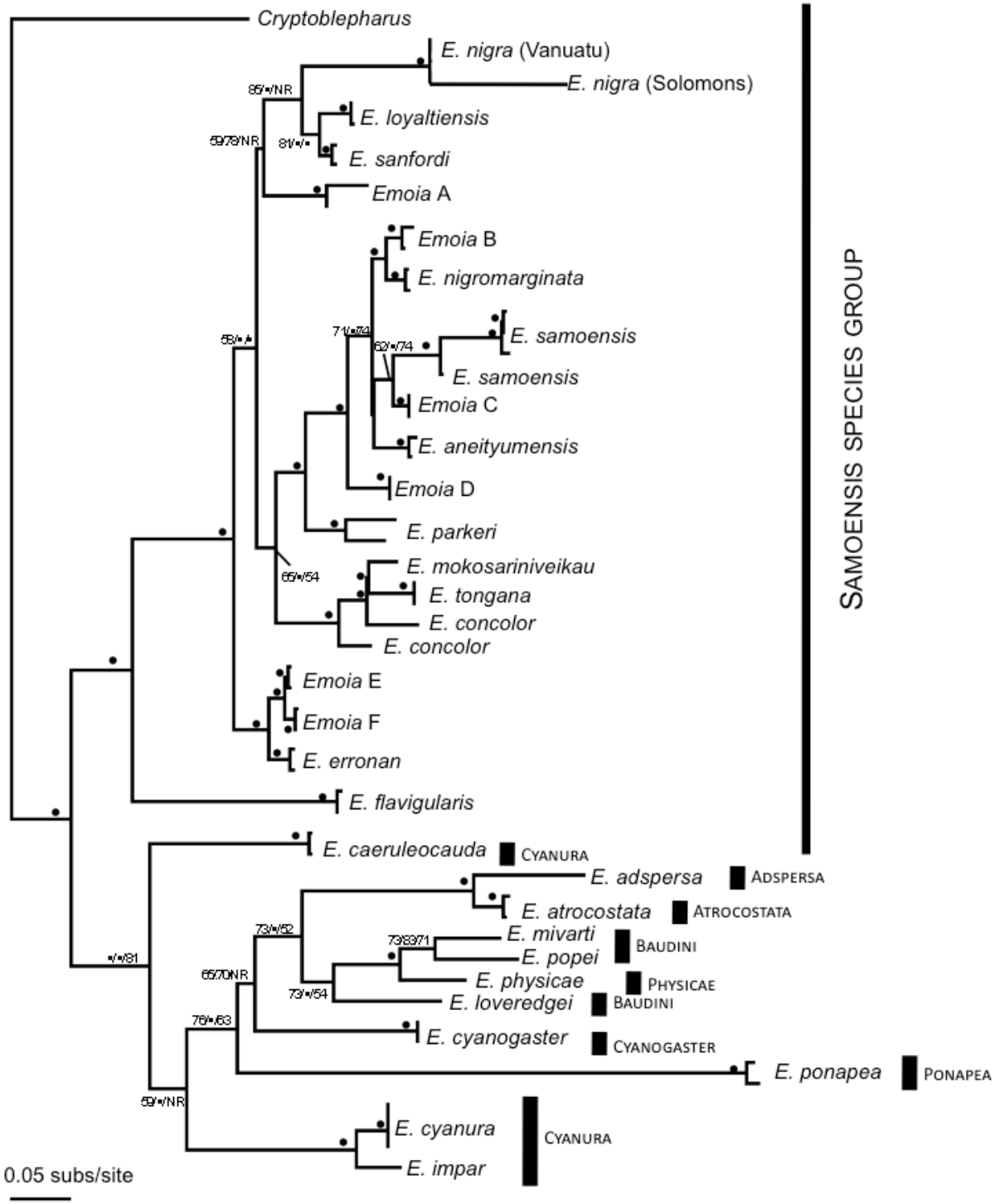
All analyses strongly support the monophyly of the *E. samoensis* group (Fig. 4.2). Many of the other lineages proposed by Brown (1991) were recovered by our analyses, although our sampling of these lineages is not thorough enough to appropriately evaluate the phylogenetic hypotheses proposed, as this was not the focus of this study. The *baudini* and *physicae* species groups, however, were not supported by our analyses: *Emoia physicae* (a member of the *physicae*-group) is included within the clade of *baudini*-group species (*E. mivarti*, *E. popei*, and *E. loveridgei*) in topologies recovered by MP, ML, and BI methods.

Samoensis and *Concolor* Subgroups

The validity of Brown's (1991) '*samoensis* subgroup' (*E. sanfordi*, *E. trossula*, and *E. samoensis*) is not supported by our data (Fig. 4.2). *Emoia sanfordi* and *E. samoensis* are not closely related, belonging to different clades within the *samoensis* group. The topology we present (Fig. 4.2) was more likely (our ML topology: -LnL= 11848.94) than topologies that were constrained to recover Brown's proposed '*samoensis* subgroup' (-LnL= 12264.47), the proposed '*concolor* subgroup' (-LnL= 12162.36) or both the '*samoensis* subgroup' and the '*concolor* subgroup' (-LnL= 12244.91) as monophyletic. A Shimodaira-Hasegawa (SH) test performed in Paup (v. 4.0b10) with full optimization and 1000 replicates (Goldman et al. 2000) indicated that the ML topology we recovered was significantly more likely than all three topologies that would support Brown's subgroups ($p < 0.001$).

We do not find support for the taxonomic distinctiveness of *E. trossula*, and consider these individuals *E. samoensis*. Our phylogeny resolved the *samoensis* group into four major groups. *Emoia loyaltiensis* (Loyalty Islands), *E. sanfordi* (Vanuatu), *Emoia* A (Vanuatu) and *E. nigra* form a monophyletic group that is sister to a larger clade containing taxa endemic to

Figure 4.2. Maximum likelihood phylogeny for the *Emoia samoensis* group using the GTR+I+G model of DNA substitution for a 2,154 bp dataset consisting of mitochondrial (Cytb, Nd4, and CO1) and nuclear (*c-mos*) DNA. Reconstructed phylogenies inferred by MP, ML, and BI methods all had the same general topology, and bootstrap values generated under ML and MP, as well as BI posterior probabilities are shown for each node: ML (bootstrap values based on 1,000 pseudoreplicates) / MP (Bayesian posterior probabilities) / MP (bootstrap values based on 500 pseudoreplicates). Support values ≥ 90% or 0.9 (•); nodes for which all three support measures are ≥ 90% or 0.9 are indicated with a single black dot (•). Nodes collapsed (i.e., the relationship among taxa was not resolved) in the MP topology are indicated with NR. Branch lengths are proportional to the number of substitutions per site (scale bar). Species groups proposed by Brown (1991) are indicated.


Cryptoblepharus
E. nigra (Vanuatu)
E. nigra (Solomons)
E. loyaltiensis
E. sanfordi
Emoia A
Emoia B
E. nigromarginata
E. samoensis
E. samoensis
Emoia C
E. aneityumensis
Emoia D
E. parkeri
E. mokosariniveikau
E. tongana
E. concolor
E. concolor
Emoia E
Emoia F
E. erronan
E. flavigularis
E. caeruleocauda
E. adspersa
E. atrocostata
E. mivarti
E. popei
E. physicae
E. loveredgei
E. cyanogaster
E. ponapea
E. cyanura
E. impar
SAMOENSIS SPECIES GROUP
CYANURA
ADSPERSA
ATROCOSTATA
BAUDINI
PHYSICAE
BAUDINI
CYANOGASTER
PONAPEA
CYANURA
0.05 subs/site

Vanuatu (*Emoia* B, *E. nigromarginata*, and *E. aneityumensis*), Fiji (*E. parkeri*, *E. mokosariniveikau*, and *E. concolor*), and taxa with distributions in Samoa, Tonga, and the Cook Islands (*Emoia* C, *Emoia* D, *E. tongana*, and *E. samoensis*). These two clades, in turn, are sister to a third clade containing three Vanuatu endemics (*E. erronan*, *Emoia* E, and *Emoia* F; Fig. 4.2). *Emoia flavigularis*, a species endemic to the Solomon Islands, is the sister taxa to all other members of the *samoensis* group (Fig. 4.2).

Sympatric species pairs were not recovered as sister taxa; all pairs of sister taxa in the phylogeny are allopatric (Fig. 4.2). To test whether a topology recovering sympatric species as sister taxa would be statistically different from our phylogeny we generated 12 additional topologies in TreeView PPC. Each topology was generated to include one pair of sympatric species recovered as sister taxa. We compared the –LnL scores of these 12 topologies against our phylogeny using a Shimodaira-Hasegawa (SH) test performed in Paup (v. 4.0b10) with full optimization and 1000 replicates (Goldman et al. 2000). Ten of the 12 topologies that would be congruent with sympatric speciation were rejected as significantly less likely than our topology (Table 4.5). Two alternative topologies were not significantly less likely: a topology that recovered *E. nigra* and *Emoia* A as sister taxa and a topology that recovered *E. nigra* and *E. sanfordi* as sister taxa.

Principle Components Analysis

The majority of the variation in morphology (91%) was explained by PC1, and PC2 explained an additional 4% of the variation. Factors loading heavily on PC1all related to lizard size, as SVL loads heavily on this axis in a positive direction, as do all other traits. PC2 describes variation in shape, particularly head shape. The three factors that loaded most heavily on PC2 were snout width, head length, and distance from nares to eye, and are associated with feeding (Table 4.6).

Table 4.5. Results of a Shimodaira-Hasegawa (SH) test comparing the likelihood scores for our maximum likelihood topology and the likelihood scores for 12 alternative topologies, each with a different sympatric species pair recovered as a pair of sister taxa. The results of the SH indicate that all alternative topologies are significantly less likely than the topology we present with the exception of two: a sister relationship between *Emoia nigra* and *Emoia* A, and a sister relationship between *E. nigra* and *E. sanfordi*.

Sympatric Pair	-LnL	p
	20621.40	
Emoia A, *E. nigra*	20649.86	.503
Emoia A, *E. sanfordi*	20711.50	**.006**
Emoia B, *E. sanfordi*	20973.58	**<.001**
E. concolor, E. parkeri	20831.35	**<.001**
E. mokosariniveikau, E. parkeri	20841.85	**<.001**
E. mokosariniveikau, E. samoensis	20950.48	**<.001**
E. nigra, E. nigromarginata	20926.81	**<.001**
E. nigra, E. sanfordi	20627.08	.925
E. nigromarginata, E. sanfordi	20973.05	**<.001**
E. parkeri, E. samoensis	20696.35	**.021**
E. samoensis, E. concolor	20964.62	**<.001**
E. tongana, Emoia C	20914.82	**<.001**

Table 4.6. Factor loadings for morphological characters on PC1 and PC2.

Character	PC1	PC2
SVL	0.983	-0.102
Trunk length	0.952	-0.136
Hind limb length	0.961	0.149
Snout-Forelimb	0.970	-.0108
Head length	0.943	-0.282
Jaw width	0.968	0.126
Head height	0.959	-.0243
Snout-eye width	0.983	.00769
Nares-eye width	0.938	-0.233
Snout width	0.891	0.425
Inter-orbital distance	0.962	0.101

Factors likely associated with arboreality (trunk length and hind limb length) also had relatively higher loading on PC2.

In general, the members of the *samoensis* group form discrete clusters in morphological space, with little overlap among species with respect to morphology (Fig. 4.3). We used a subset of these data to more closely examine how morphology is partitioned in sympatric and allopatric taxa. Species that have been recorded from the same island within an archipelago were considered sympatric. Within the Vanuatu Archipelago and the Loyalty Islands, members of the *samoensis* group occur on most islands. In these island groups, taxa that are always allopatric with all other members of the *samoensis* group had a higher degree of morphological overlap with respect to morphology with respect to all other Vanuatu *samoensis* group species (Fig. 4.4a), suggesting either morphological conservatism or repeated evolution of a particular suite of morphological traits. For sympatric taxa, no overlap was detected among co-occurring species (Fig. 4b-d). Differences in PC1 scores (characters reflecting body size) account for the separation between *E. nigromarginata*, *Emoia* A, *Emoia* B and *E. sanfordi* (Fig. 4.4b-c), whereas morphological differences associated with feeding ecology (PC2) are responsible for the morphological differences between the arboreal *E. sanfordi* and the terrestrial *E. nigra* (Fig. 4.4d).

Use of Morphospace by *Emoia*

In Vanuatu, it is clear that much of the available morphological space is occupied by *Emoia* (Fig. 4.4); the two measures of morphology (PC1 and PC2) are not correlated. A very different relationship was recovered for *samoensis* group species outside of Vanuatu. For *samoensis* group species in Fiji, Samoa, and Tonga, a negative relationship is observed between body size and morphological traits associated with feeding ecology, microhabitat use and dietary breadth

Figure 4.3. Morphological traits of the members of the *Emoia samoensis* group, shown as the relationship between PC1 (body size) and PC2 (traits associated with feeding ecology, microhabitat use, and dietary breadth). The geographic distribution of each species is shown in the legend, and the following abbreviations are used: Solomon Islands (SI), Oceania (OC), and Cook Islands (CI). Oceania is used to indicate that the species has a relatively broad distribution in the region, occurring in the Solomon Islands, Vanuatu, Fiji, and Samoa.

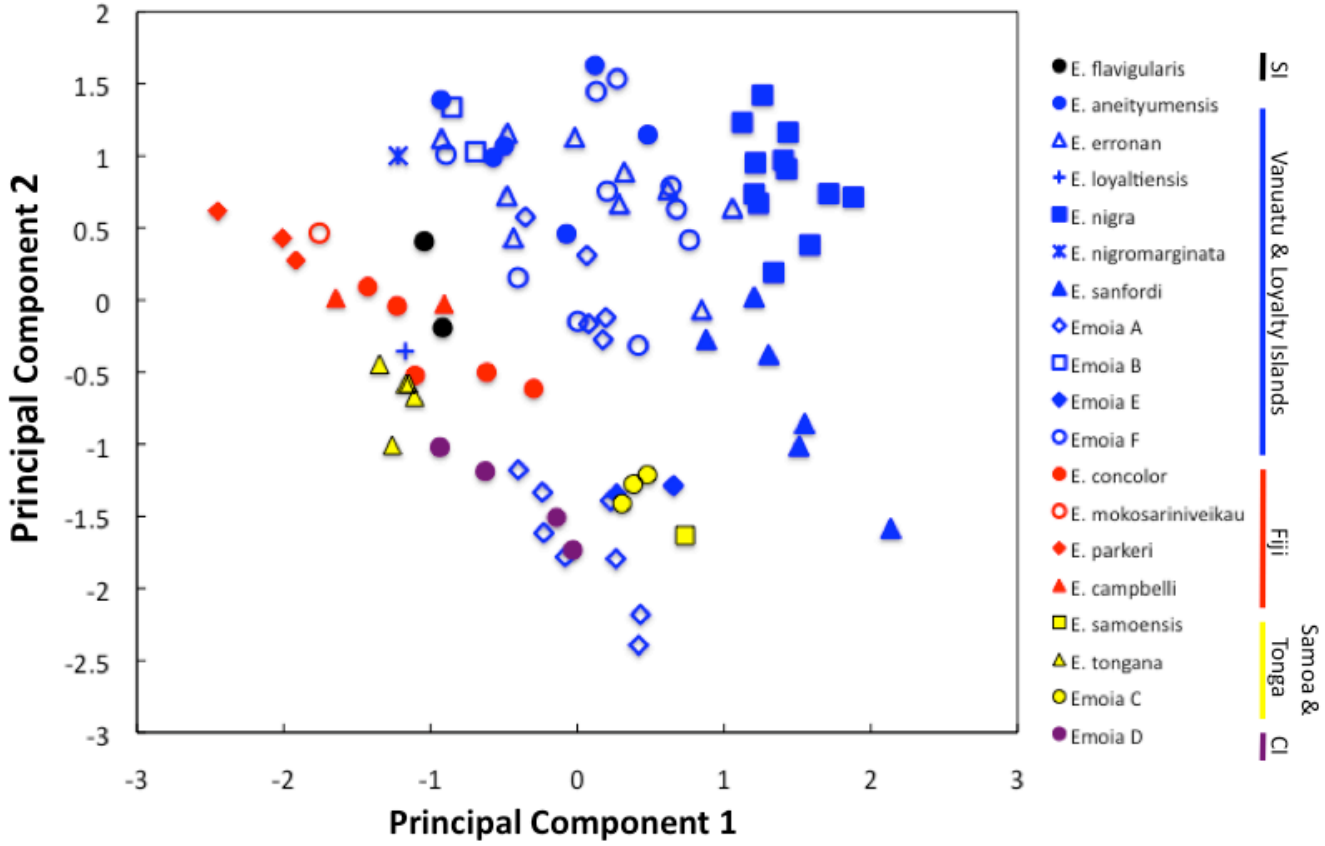

Principal Component 2
Principal Component 1
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3
-2
-1
0
1
2
3
E. flavigularis
E. aneityumensis
E. erronan
E. loyaltiensis
E. nigra
E. nigromarginata
E. sanfordi
Emoia A
Emoia B
Emoia E
Emoia F
E. concolor
E. mokosariniveikau
E. parkeri
E. campbelli
E. samoensis
E. tongana
Emoia C
Emoia D
SI
Vanuatu & Loyalty Islands
Fiji
Samoa & Tonga
CI

Figure 4.4. Morphological traits of the members of the *Emoia samoensis* group occurring in Vanuatu, shown as the relationship between PC1 (body size) and PC2 (traits associated with feeding ecology, microhabitat use, and dietary breadth). (A) Species from Vanuatu that are allopatric with all other *samoensis* group members. Three different sympatric species assemblages are shown in panels B-D, as follows: (B) *E. nigromarginata, E. sanfordi*, and *Emoia* A; (C) *E. nigromarginata, E. sanfordi*, and *Emoia* A; (D) *E. nigra, E. nigromarginata*, and *E. sanfordi*.

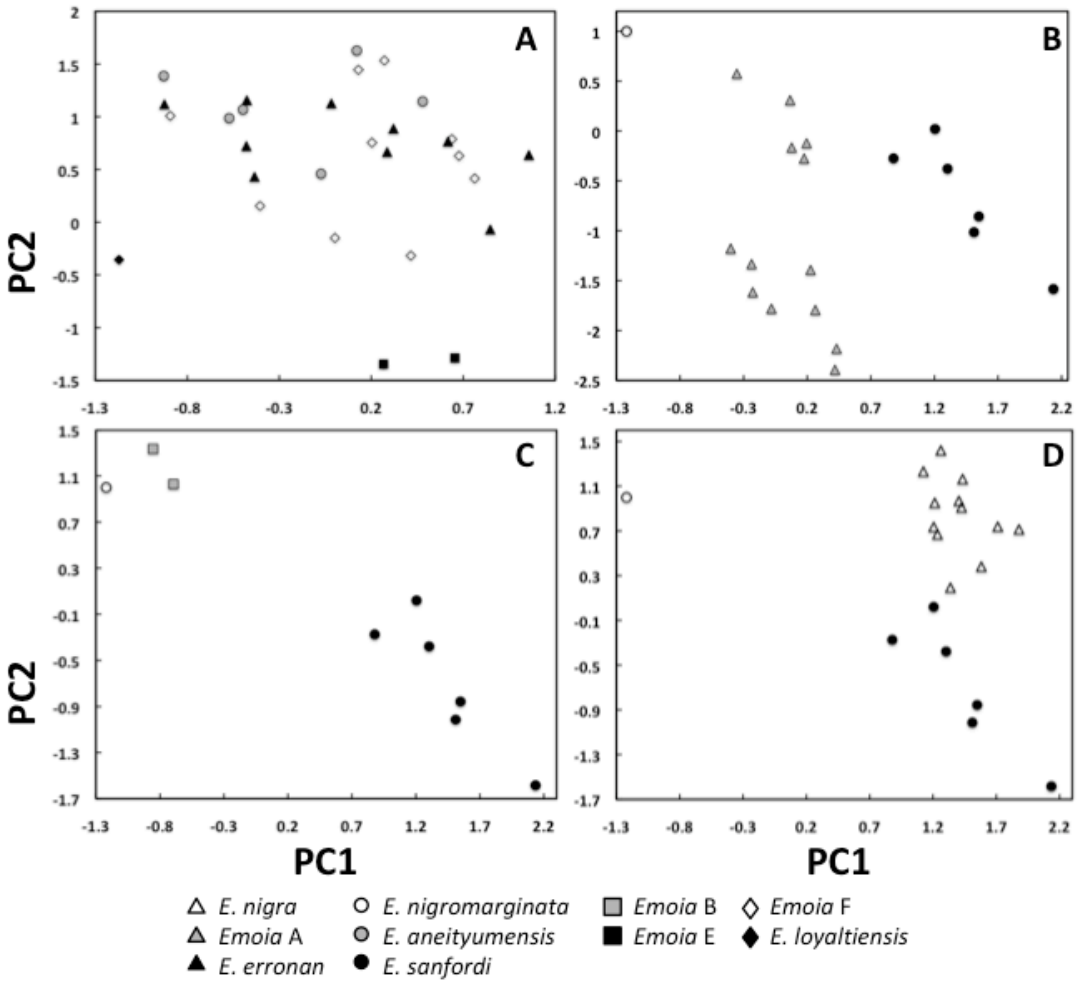
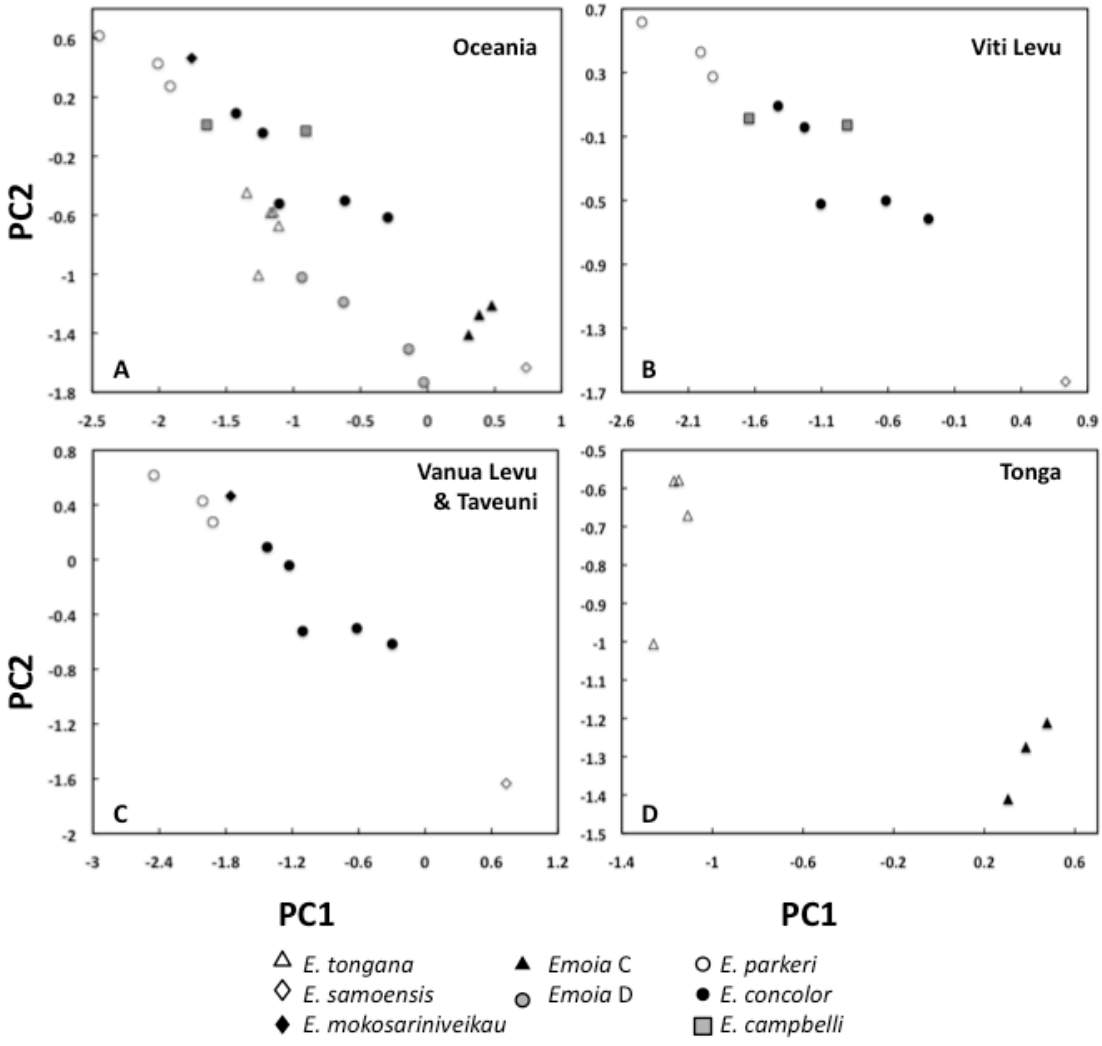

A
B
C
D
PC1
PC2
E. nigra
Emoia A
E. erronan
E. nigromarginata
E. aneityumensis
E. sanfordi
Emoia B
Emoia E
Emoia F
E. loyaltiensis

Figure 4.5. Morphological traits of the members of the *Emoia samoensis* group occurring in the islands of Fiji, Tonga, Samoa, and the Cook Islands, shown as the relationship between PC1 (body size) and PC2 (traits associated with feeding ecology, microhabitat use, and dietary breadth). (A) All *Emoia samoensis* group species from Fiji, Tonga, Samoa, and the Cook Islands. (B) The assemblage of *Emoia samoensis* group species that are sympatric on Viti Levu, Fiji; (C) The assemblage of *Emoia samoensis* group species that are sympatric on Vanua Levu and Taveuni Islands, Fiji; (D) The assemblage of *Emoia samoensis* group species that are sympatric on Tonga.

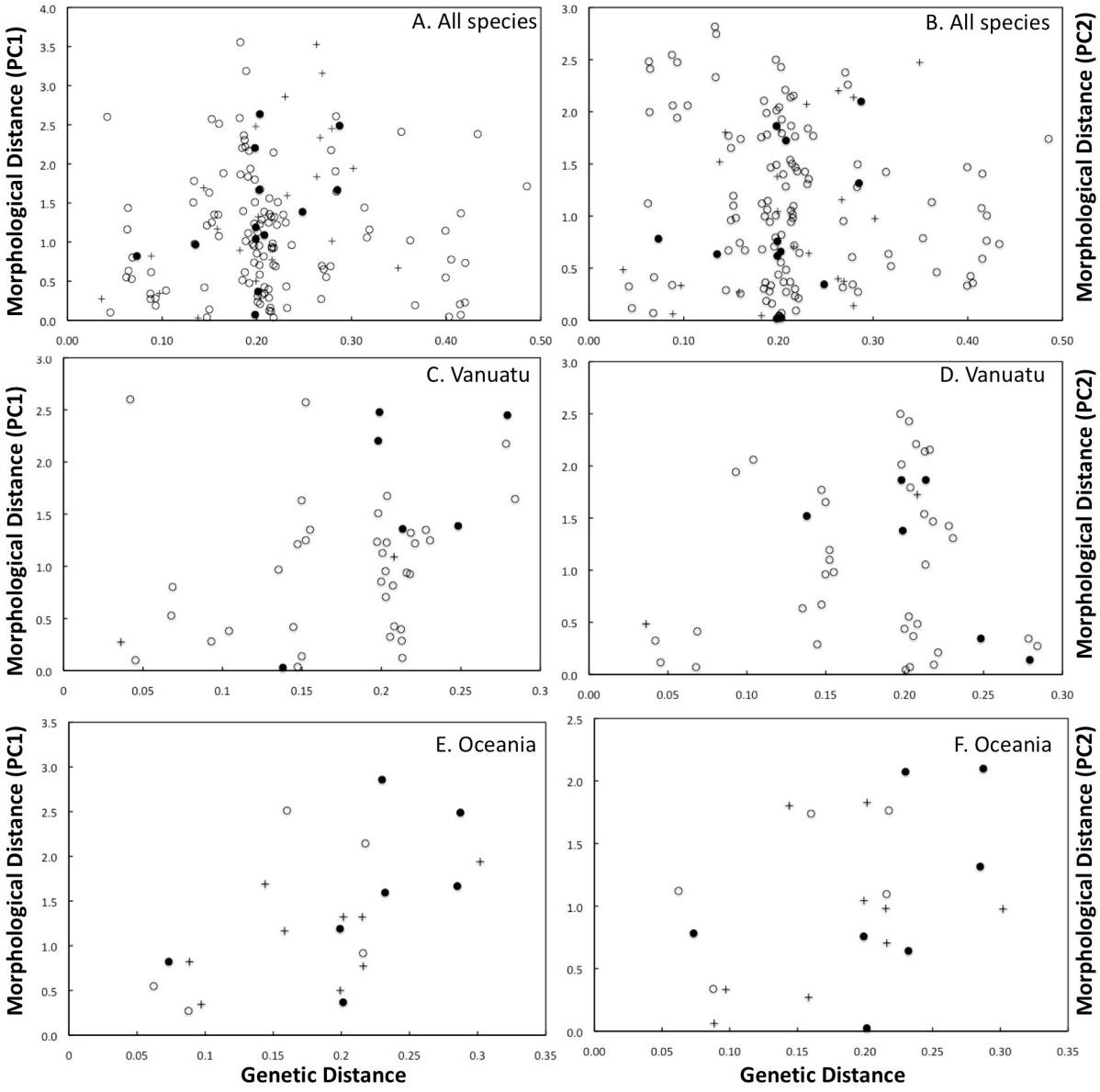

Oceania
A
Viti Levu
B
Vanua Levu & Taveuni
C
Tonga
D
PC1
PC2
E. tongana
E. samoensis
E. mokosariniveikau
Emoia C
Emoia D
E. parkeri
E. concolor
E. campbelli

(PC2), suggesting that perhaps in these islands there is still morphological space available for diversification, or perhaps these morphologies and their associated niches are filled by other groups (Fig. 4.5). Sympatric species are well separated morphologically (by both body size and feeding ecology and dietary breadth associated characters) on the major islands of Fiji and Tonga (Fig. 4.5b-d). There are two instances of possible, overlap with respect to morphology: *E. parkeri* and *E. mokosariniveikau* appear to occupy the same morphological space (Fig. 4.5c), as do *E. campbelli* and *E. concolor* (Fig. 4.5b). Although we have considered these species pairs to be sympatric based on our criteria for sympatry (distribution on the same island), it is not clear if they do in fact co-occur, due to incomplete knowledge of the distribution of many species of *Emoia* within Fiji. At the present time, *E. mokosariniveikau* is known only from a single specimen, so the extent to which it may be sympatric with *E. parkeri* is unclear. *Emoia campbelli* is known only from the type locality, the montane cloudforest of the Monasavu area on Viti Levu, Fiji. Although *E. concolor* has a broad distribution on Viti Levu, it is a forest generalist in its habitat requirements (Zug 1991; Morrison 2003), and the degree of which *E. concolor* and *E. campbelli* are sympatric relies upon the degree of habitat specialization of *E. campbelli*.

Matrix Regression of Morphological Distance on Genetic Distance

Patristic distances generated from our phylogeny were not correlated with morphological distances (PC1: z=124.396, p=0.276; PC2: z=20.405, p=0.754). Sympatric pairs of *samoensis* group species had intermediate genetic distances (Fig. 4.6a,b). Most sympatric species pairs were also found to have moderate to high levels of divergence with respect to both body size (Fig. 4.6a) and morphology associated with feeding ecology and dietary breadth (Fig. 4.6b), with a few exceptions. Sympatric species pairs were significantly more differentiated by body size

Figure 4.6. Results of Mantel matrix regressions of morphological distance (Euclidean distance matrices for each principle component on the mean taxon principle component scores) on genetic distance (mean pairwise patristic distances from the ML multi-locus phylogeny). Morphological traits associated with size (PC1; left column of panels) and shape (PC2; right column of panels) were regressed independently against genetic distance. In all panels, open circles represent an allopatric species pair and closed circles represent a sympatric species pair; cases of uncertainty are indicated with '+'. The relationship between body size (PC1) and genetic distance is shown for (A) all *Emoia samoensis* group species; (C) *samoensis* group species in Vanuatu; and (E) *samoensis* group species in Oceania (Fiji, Tonga, Samoa, and the Cook Islands). The relationship between shape (PC2) and genetic distance is shown for (B) all *Emoia samoensis* group species; (D) *samoensis* group species in Vanuatu; and (F) *samoensis* group species in Oceania (Fiji, Tonga, Samoa, and the Cook Islands).


A. All species
B. All species
C. Vanuatu
D. Vanuatu
E. Oceania
F. Oceania
Morphological Distance (PC1)
Morphological Distance (PC2)
Genetic Distance

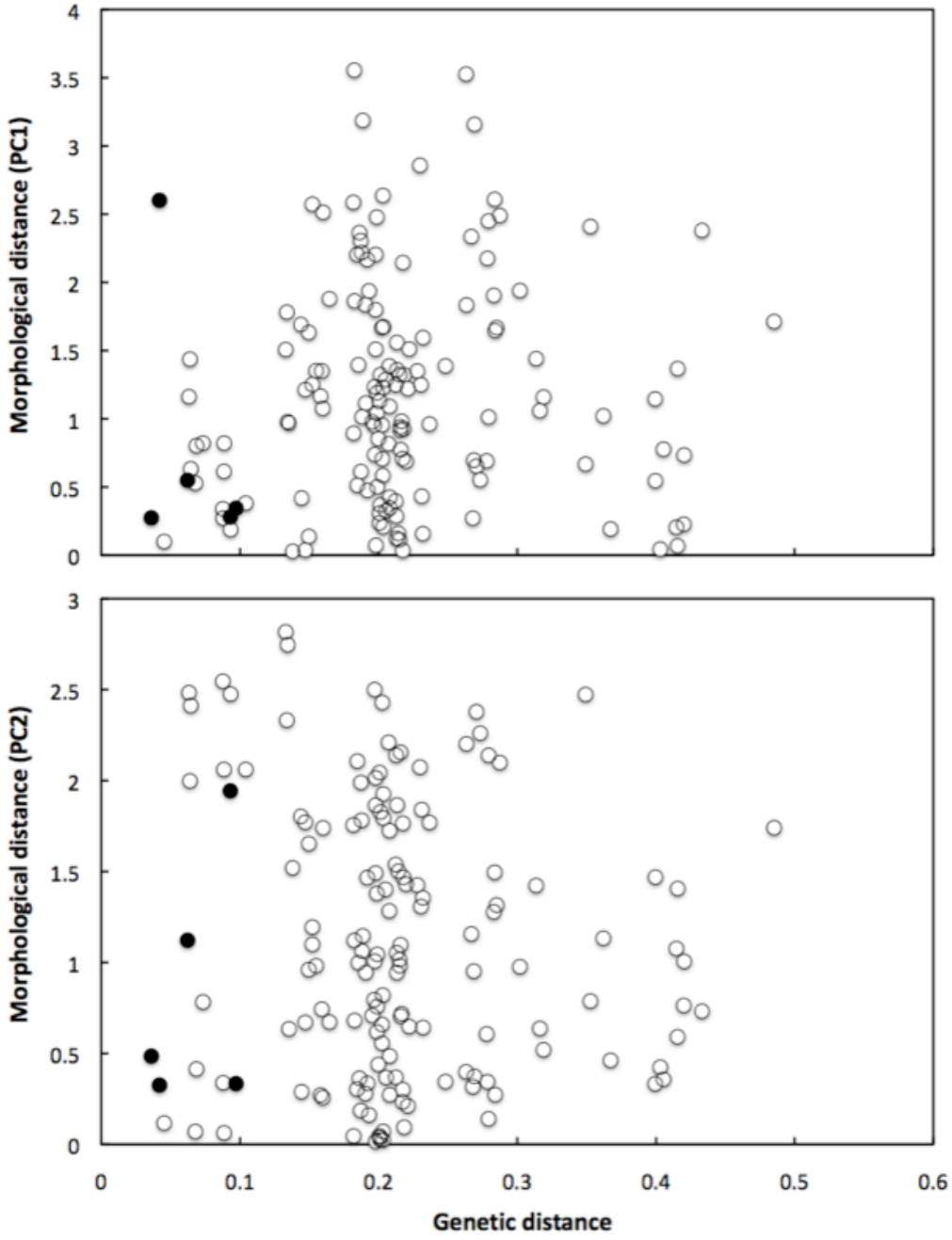
that allopatric species pairs (p=0.04), but the difference along PC2 between sympatric and allopatric species pairs was not significant (p=0.41). Within individual archipelagos, the pattern is slightly different. In Vanuatu, species pairs with lower levels of genetic divergence are never sympatric (Fig. 4.6c,d), and sympatric pairs are strongly differentiated by either body size (Fig. 4.6c), by the ecologically relevant morphological characters associated with PC2 (Fig.4.6d) or both. In Fiji and Tonga, sympatric taxa do not show stronger morphological differentiation than allopatric taxa with comparable levels of genetic divergence, and the relationship between level of genetic divergence and morphological differentiation appears almost linear, with morphological differentiation increasing with genetic divergence (Fig. 4.6 e,f). While these relationships for subgroups of species could not be evaluated with Mantel tests, because they do not include all possible pairwise comparisons among their constituent species, the pattern in Fiji and Tonga is more consistent with a non-ecological mechanism of divergence.

In general, sister taxa were not highly differentiated from each other with respect to morphology (Fig. 4.7). Pairs of sister taxa that varied from each other morphologically did not tend to be sympatric, suggesting that adaptive sympatric speciation does not play a role in the *Emoia samoensis* group. Instead, these sister taxa were distributed on neighboring archipelagos such as *E. sanfordi* and *E. loyaltiensis* (separated by body size; Fig. 4.7a) or *E. mokosariniveikau* and *E. tongana* (separated by morphology associated with feeding ecology; Fig. 4.7b) or occur on neighboring islands within an archipelago, such as *Emoia* E and *Emoia* F in Vanuatu (differentiated by morphology associated with tropic level; Fig. 4.7b).

DISCUSSION

Monophyly of the *Emoia samoensis* group suggests that this lineage of relatively large, primarily arboreal scincid lizards represent a radiation of species in the islands of the southwest Pacific

Figure 4.7. Results of Mantel matrix regressions of morphological distance (Euclidean distance matrices for each principle component on the mean taxon principle component scores) on genetic distance (mean pairwise patristic distances from the ML multi-locus phylogeny). These data show the relationship between morphological distance and genetic distance for pairs of sister taxa and for non-sister species pairs. In both panels, black circles indicate sister taxa, and open circles represent all other comparisons.


Morphological distance (PC1)
4
3.5
3
2.5
2
1.5
1
0.5
0
Morphological distance (PC2)
3
2.5
2
1.5
1
0.5
0
0
0.1
0.2
0.3
0.4
0.5
0.6
Genetic distance

Ocean. The geographic distribution of these species suggests that this lineage has diversified on these remote islands, as all members of this lineage occur on oceanic islands in Oceania and Melanesia (Fig. 4.1), and the topology of the recovered phylogeny suggests a single invasion of the region by an ancestral taxon (Fig. 4.2). The relationship of the members of the *samoensis* group to the other species of *Emoia* was not resolved by our phylogeny, as a large clade containing all other species of *Emoia* sampled was recovered as the "sister group" to the *samoensis* group. A close relationship between the *samoensis* group and the *cyanura* group was previously suggested based on morphology (Brown 1991), and is not rejected by our data. A shared common ancestor shared by these two lineages would, therefore, likely have originated in the islands of the Solomon Islands, a biogeographic scenario that is congruent with our phylogeny, as *E. flavigularis*, a species endemic to the Solomon Islands, was recovered as the sister taxa to a clade containing the remaining members of the *samoensis* group (Fig. 4.2).

The recovered phylogeny does not support a simple stepping stone model of colonization for the *Emoia samoensis* group in the Pacific. Placement of *E. flavigularis* (Solomon Islands) as the sister species to all other members of the species group and *E. nigra* (broader distribution, including the Solomon Islands) as the sister taxa to a clade containing the remainder of the species group (except *E. flavigularis*) provides support for a single invasion of the Pacific, likely from an ancestor in the Solomon islands or New Guinea. The remainder of the phylogenetic relationships, however, suggests a more complex colonization history for this group of lizards in Oceania. Island groups do not represent monophyletic lineages as would be expected if the *samoensis* group composition of each archipelago was the result of a single colonization event, followed by in situ speciation. Although some clades do show this pattern (for example *Emoia* E, *Emoia* F, and *E. erronan* form a monophyletic group, and are all endemic to the islands of the Vanuatu Archipelago), other clades contain species from throughout Oceania, and suggest

evidence of the colonization of Vanuatu and Fiji by lineages present in the Cook Islands and Tonga. This pattern is congruent with the findings of Filardi and Moyle (2005), who found that a uni-directional 'stepping stone' model of colonization of the islands of the Pacific Ocean did not reflect the evolutionary history of monarch flycatcher birds. Like monarch flycatchers, in the *Emoia samoensis* group we also find evidence for the evolution of species within these remote islands, and the subsequent re-invasion of previously colonized islands by forms derived from far flung, isolated Pacific forms, rather than 'mainland' ancestral forms.

We do not find evidence for sympatric speciation within this lineage. Only one pair of sister taxa are sympatric: *Emoia* B and *E. nigromarginata*. These two species are weakly differentiated with respect to body size (Fig. 4.4c), but this difference is not great even when genetic distance is accounted for (Fig. 4.7). Although we have considered these two species to be sympatric, we are uncertain as to the degree to which they overlap in an ecologically meaningful way. Although both species occur on the same island, and use the same type of forest and microhabitat, the two species have not been observed syntopically (A. Hamilton, pers. observation). Additionally, *E. nigromarginata* does not appear to be common at sites where *Emoia* B was observed, and neither species was particularly abundant on the island on which they co-occur (A. Hamilton, pers. observation). No other pairs of sister taxa have overlapping distributions, suggesting that sympatric speciation is unlikely. These findings are congruent with a previous study of island birds which examined the number of endemic species pairs with sympatric distributions and found few cases of sympatry in sister taxa and no evidence for sympatric speciation (Coyne and Price 2000).

The geographic distribution of sister taxa suggests a possible role for peripatric speciation in the diversification of this species group. One pair of sister taxa (*Emoia* E and *Emoia* F) occurs on adjacent islands, and this pair of taxa is, in turn, sister to *E. erronan*, a species which occurs

on two islands adjacent to the distributions of *Emoia* E and *Emoia* F. Additionally, the previously discussed distribution of *Emoia* B and *E. nigromarginata* could also support a speciation event in peripatry.

Members of the *samoensis* group are generally well differentiated morphologically, and members of a species cluster in morphospace. When principal component 2 is plotted against principal component 1, species that have narrow distributions (for example, those endemic to a single island) and that do not co-occur with other members of the *E. samoensis* group tend to cluster in the middle of the morphospace occupied by this species group. Species with broader geographic distributions, or those that are sympatric with another *samoensis* group species tend to occur along the margins of this morphospace, and appear more morphologically differentiated from other species (Fig.4.3). This pattern is more obvious when the species from Vanuatu are examined more closely. Vanuatu *samoensis* group species that are always allopatric with respect to other *samoensis* group species have morphological overlap with each other (Fig. 4.4a). Species that occur sympatrically are well differentiated from one another; there is no evidence for overlap among co-occurring species (Figs. 4.4b-d). In general, these species are separated along PC1 (body size) and PC2 (feeding ecology and habitat use). Likewise, sympatric species are well differentiated in the islands of Fiji and Tonga and are generally separated from each other by factors contributing to both PC1 and PC2, as they are in Vanuatu (Figs. 4.6b-d).

In contrast, to the distribution of *samoensis* group morphologies in Vanuatu, the *samoensis* group members in Fiji and Tonga do not utilize all available morphologies, and the relationship between PC1 and PC2 appears linear, as if head-shape morphologies that influence feedings and diet simple change as a function of body size (Fig. 4.5a). We suggest that this pattern reflects two factors that provide insight into the mechanisms of speciation in the *Emoia samoensis* group. First, there are 9 species of *Emoia* in Vanuatu that are part of this *samoensis*

group lineage, and within this island group the *samoensis* group lineages accounts for 56% of scincid lizard diversity and 16% of the total native lizard diversity. The *samoensis* group represents 60% of scincid lizard diversity in Fiji and 44% of scincid lizard diversity in Tonga, and 33% and 27% of overall lizard diversity in Fiji and Tonga, respectively (Hamilton et al. 2008b). Both Fiji (18 species) and Tonga (15 species) have lower lizard species richness, despite the occurrence of a third lizard family (Iguanidae) in each of these island groups. Perhaps genera not occurring in Vanuatu (*Leiolopisma* and *Tachygia*) or families (Iguanidae) are occupying some of the morphospace in Fiji and Vanuatu, thus preventing *Emoia* from evolving these morphologies. Alternatively, the presence of unoccupied morphospace in Fiji and Tonga may simply be a by-product of lower diversification within the *Emoia samoensis* group in these island groups.

The strong relationship between body size and shape, particularly head shape, is the evolutionary pattern we would expect to recover in the absence of strong selection on morphology. The lack of correlation of these morphological characters seen in the *samoensis* group species from Vanuatu could result from strong selection on morphological traits associated with dietary breadth and climbing ability, allowing the differentiation observed among sympatric species that is likely necessary for co-occurrence. The relationship between both measures of morphological distance (size and shape) with genetic distance is suggestive of the role of ecology in diversification in this species group. Within the samoensis group in general, and the Vanuatu species in particular, sympatric taxa are rarely recently diverged. In cases where sympatric species have only a moderate level of genetic diversity, the sympatric pair is generally strongly morphologically differentiated (Fig. 4.6). The increased morphological differentiation relative to time since speciation for sympatric taxa is suggestive of the role of ecology on the evolution of morphology in these taxa, especially in light of the evidence for morphological conservatism in

Emoia and other Pacific scincid lizards (Austin 1995; Bruna et al. 1995; Bruna et al. 1996b; Austin and Zug 1999; Smith et al. 2001; Smith et al. 2007). This conservatism is apparent within our data for the *samoensis* group as well (Fig. 4.7), as species pairs with a very low level of morphological divergence may have high genetic divergence, reflecting a history of morphological stasis.

The combination of morphological stasis combined with the potential for rapid evolution of morphological traits, potentially as a result of divergent selection, has created taxonomic confusion with respect to defining species boundaries among the *Emoia samoensis* group members has been difficult (Zug 1985, Zug 1991; Zug and Ineich 1995; Austin and Zug 1999). The phylogeny presented here, as well as the inferences made about the evolution of diversity in this diverse group of lizards, is an important step in understanding how species radiations arise and diversify.

CHAPTER 5: *EMOIA SANFORDI* IN THE VANUATU ARCHIPELAGO

Islands have played a crucial role in our understanding of speciation, the fundamental process that generates biological diversity. Organisms that arrive on isolated oceanic islands are subject to the same evolutionary processes that occur in mainland environments. However, factors such as the smaller population size of island faunas, increased isolation of insular populations, and unoccupied niches frequently increase the rate at which diversification, extinction, and other evolutionary phenomenon occur (Ziegler 2002). Due in part to the rapid pace of evolution on islands and sterile nature of newly emergent oceanic islands, island systems have acted as 'natural laboratories' allowing biologists to develop and test hypotheses related to the mechanisms responsible for speciation and extinction. Due to the relative simplicity of island systems compared to continental regions, oceanic islands provide biologists an opportunity to observe patterns resulting from these evolutionary processes without confounding factors such as long periods of geologic time or dramatic changes in geography.

Several archipelagos have been the primary backdrop for evolutionary and ecological studies during the past century: the Galapagos Islands (Darwin 1859; Grant 1986; Sequeira 2000; Grant 2001), the Caribbean (Roughgarden 1995; Losos and de Queiroz 1998; Losos et al. 1998), Hawaii (Kaneshiro 1988, Kaeshiro et al. 1995; Shaw 1996; Fleischer et al. 1998; Shaw 2002), and the Canary Islands (Thorpe et al. 1994; Thorpe and Malhotra 1998; Emerson et al. 2000a; Emerson et al. 2000b). These studies have provided amazing insight into the processes of colonization and adaptive radiation, one of the landmarks of island evolution. Through studying island faunas, biologists have also gained an understanding of the importance of even low levels of gene flow to counteract potential diversification, as well as the mechanisms such as behavioral changes that can promote speciation, even in the absence of a physical barrier to interbreeding

among incipient species. Yet, many characteristics of the well-studied island systems create limitations influencing our ability to detect the underlying fundamental mechanisms generating diversity in these systems. The Galapagos Islands and Hawaii are both geologically old relative to other island systems. This long time period since emergence and complex geological history (e.g. hotspot conveyor belt formation) has resulted in an intricate history of island emergence and submergence. The combination of geologic age and complexity is undoubtedly responsible for the incredible diversity due to a combination of biotic accumulation and in-situ cladogenesis, but time also confounds the interpretations of patterns of colonization, speciation, and extinction.

Vanuatu is a geologically young island group (all islands continually emergent < 2 million years), permitting interpretation and analysis of intra-archipelago variation during a nascent radiation. It is difficult make comparisons among old, tectonically complex island groups. To determine the underlying evolutionary patterns and to uncover the **general** patterns of diversification in island systems therefore, it is necessary to examine recently emergent oceanic islands with taxa in the early stages of diversification and radiation. Due to its brief history of emergence, simple tectonic history, oceanic origin, and degree of isolation, the Vanuatu Archipelago (Fig. 5.1) is a good model system in which to untangle the complex processes of colonization, population differentiation and extinction before millions of years of subsequent evolution, colonization, submergence, and extinction obscure the initial patterns of diversification.

The Vanuatu Archipelago is an ideal island group in which to examine questions associated with the role of island systems in promoting differentiation and speciation. As Vanuatu is an oceanic archipelago, its fauna is derived in two ways: (1) over water dispersal and (2) speciation. This is a geologically young island group (most islands emergent < 2 mya), permitting greater ease in understanding patterns of intra-archipelago variation as factors such as

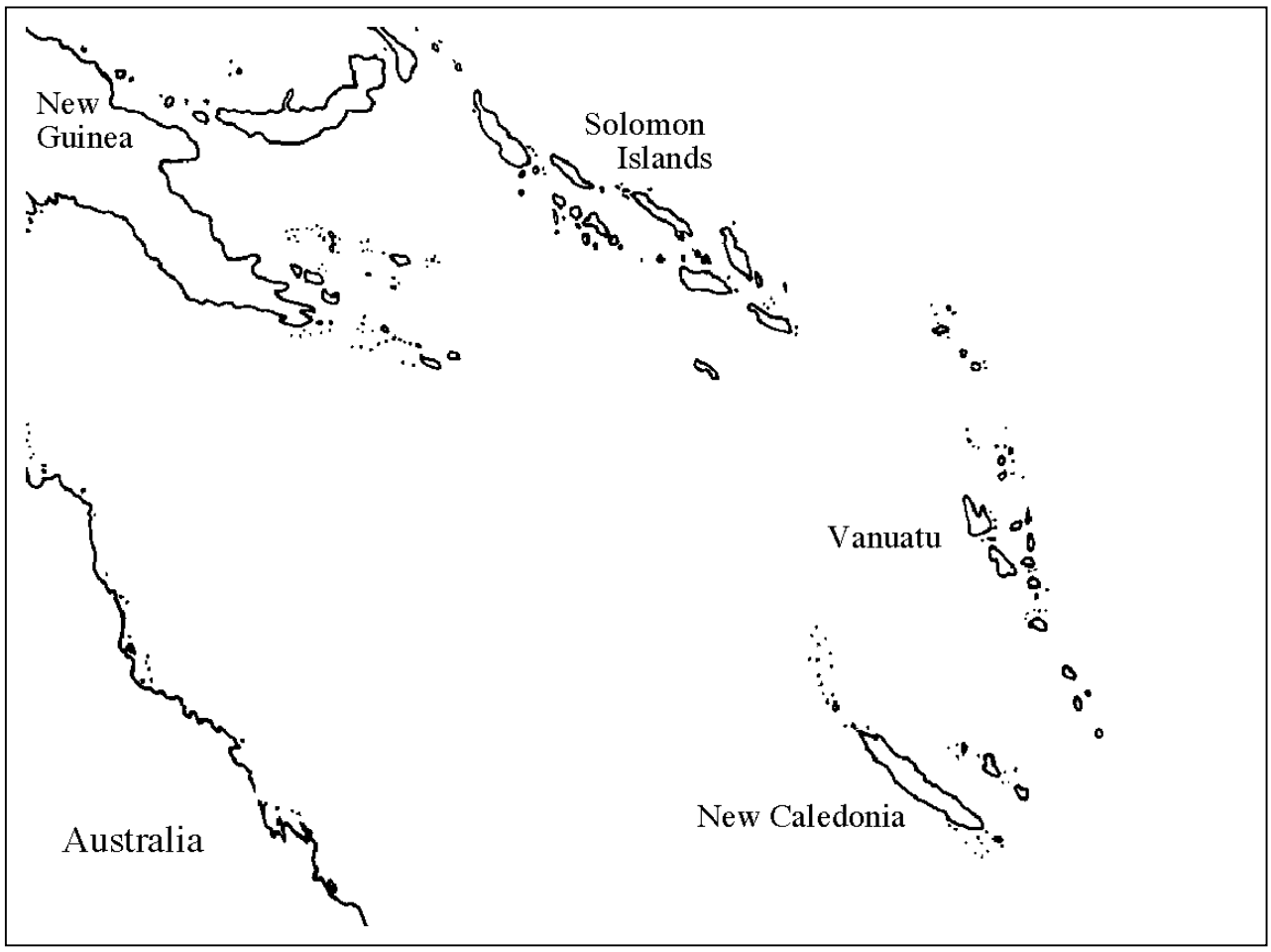


Figure 5.1 The Vanuatu archipelago in the southwestern region of the Pacific Ocean, shown in relation to Australia, New Guinea, the Solomon Islands and New Caledonia.

island age or associations with ancient landmasses will not confound interpretation. The structure of the Vanuatu Archipelago also lends itself to an examination of the role of factors such as island size and age, isolation, and habitat diversity on population differentiation and speciation as it contains multiple islands of the same approximate ages that differ in size, elevation, or degree of isolation. Additionally, the history of sea-level changes and previous connections among islands during periods of lowered sea levels is relatively well known (Mead et al. 2002).

The Vanuatu Archipelago is one component of an island arc system which extends from New Britain to the Solomon Islands and also includes Fiji, Tonga, Vanuatu, and the Kermadec Islands and formed as early as the Cretaceous (Carney et al. 1985). Vanuatu was originally located a few hundred kilometers further to the northeast of its present day location, directly between the Solomon Islands and Fiji, and it has been suggested that this archipelago played a significant role for biota colonizing the southwest Pacific. Vanuatu may have acted as a stepping-stone for Australasian flora and fauna from New Guinea and Australia, enabling many taxonomic groups to reach Fiji and the islands east of Fiji (DeBoer 1995). However, a reversal in polarity of the Fiji and Vanuatu section of the arc 8-10 mya caused Vanuatu to migrate southwest (Malahoff et al. 1982; Carney et al. 1985). Rotation of the Vanuatu Archipelago removed it from the colonization pathway of Fiji from the Solomon Islands and created the North Fiji Basin. Breakup of the arc likely contributed to regional diversity by promoting vicariant speciation events (DeBoer 1995).

The current geology of the Vanuatu Archipelago results from three distinct volcanic provinces: western, eastern, and central belts (Macfarlane et al. 1988). Each province has resulted in the formation of several islands within the archipelago (Fig. 5.2), and is associated

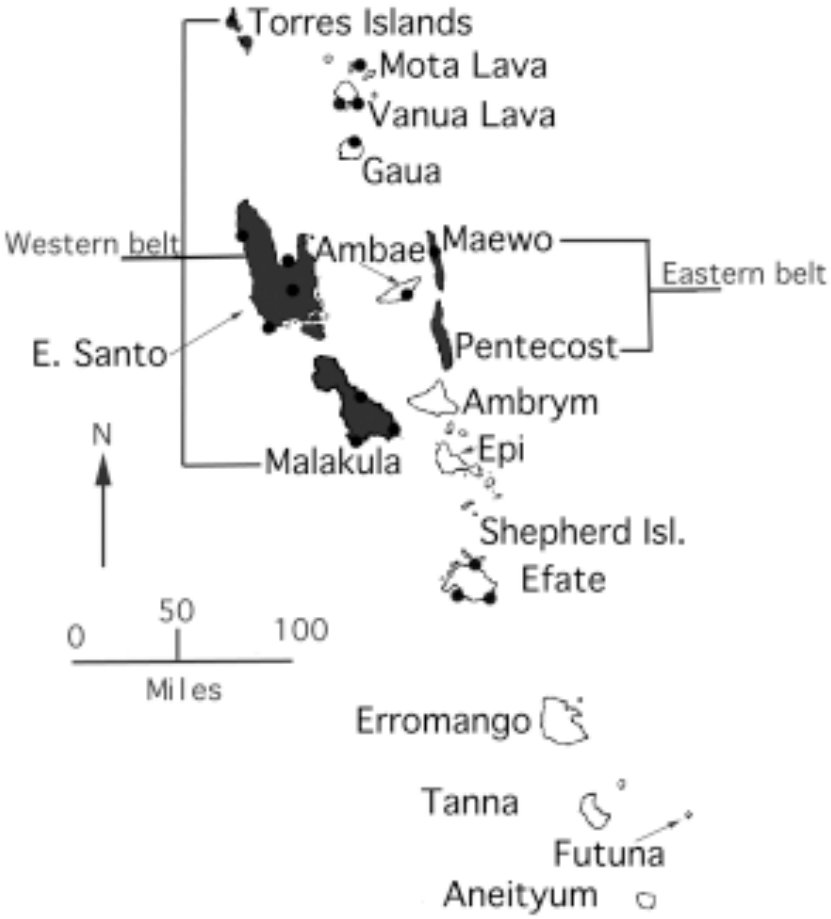


Figure 5.2. The Vanuatu Archipelago, indicating geologic provinces resulting from three periods of volcanisms and associated with island age. The oldest islands in the group, the islands of the western belt (shaded) include the Torres Group, Espiritu Santo, and Malakula. The eastern belt (shaded) consists of Maewo and Pentecost. The remainder of the islands in the Vanuatu Archipelago make up the islands of the central chain (not shaded); these islands are the youngest and most recently emergent islands in the archipelago.

with the movements of particular structural entities (such as crustal ridges or frontal arc movements) that create volcanism and island formation (Carney et al. 1985). The oldest islands in the Vanuatu Archipelago are Espiritu Santo, Malakula, and the Torres Islands (those of the Western Belt), which date from a period of volcanism in the Miocene (11-14 mya). Formation was followed by periods of uplift and erosion, and these islands likely became emergent within the last 2 mya (Carney et al. 1985; Greene et al. 1988a; Macfarlane et al. 1988). The islands of Pentecost and Maewo (Eastern Belt) formed next, resulting from a period of volcanism 14-8 mya. During the late Miocene (8-6 mya) these islands rapidly evolved as a result of sea floor spreading, and likely emerged after 1.8 mya (Carney et al. 1985). The majority of islands in the archipelago belong to the central belt. These islands were formed as a result of a period of volcanism that began as early as 3.5 mya and continues to the present (Carney et al. 1985). The dates of island formation and emergence vary among islands in this group, but all have become emergent relatively recently, likely in the last 1 mya.

In the islands of Oceania, lizards in the genus *Emoia* represent an important component of the terrestrial vertebrate fauna, with multiple species occurring on most islands in the region (Brown 1991; Zug and Ineich 1995; Hamilton et al. 2008b). Recent molecular data and archipelago-wide survey data indicate that species of *Emoia* account for the majority of the native scincid lizard fauna (88%) of the Vanuatu Archipelago, and over half (54%) of the currently recognized native terrestrial squamate reptile fauna of this island arc (Hamilton et al., unpublished data). Many Vanuatu *Emoia* are part of a monophyletic radiation of large-bodied, primarily arboreal lizard species referred to as the *samoensis* group (Brown 1991); in fact, species richness within this lineage is greatest within in the Vanuatu Archipelago and the islands of Fiji (Hamilton et al. 2008b). This radiation of *Emoia* accounts for over one-third (35%) of the overall native terrestrial squamate reptile diversity of the Vanuatu Archipelago, and eight of the

nine species that have distributions including Vanuatu in this lineage are restricted to the Vanuatu Archipelago.

The high species diversity and level of endemism seen in *Emoia* within Vanuatu suggests the archipelago plays a biogeographic role in the generation and maintenance of species diversification for this genus. To understand how species diversity has accumulated in Vanuatu, I determine genetic structure and diversity within and among island populations of a species of *Emoia* with a broad distribution in the Vanuatu archipelago. *Emoia sanfordi* is one of the 19 members of the *samoensis* species group, the lineage representing more than one-third of the terrestrial squamate fauna of Vanuatu. This species is a large (adult SVL 68.3-115 mm), arboreal skink endemic to the central and northern islands of the Vanuatu Archipelago (Brown 1991; Hamilton et al. 2008a). This species has the broadest distribution within Vanuatu of the members of the *samoensis* group radiation, enabling a comparison of genetic diversity and examination of genetic structure across a broad geographic range in this island group and allowing inferences to be made regarding the generation of diversity and within this island system. As *E. sanfordi* does not occur outside of the islands of Vanuatu, patterns of genetic structure and levels of genetic diversity recovered in this species likely reflect processes that have occurred within Vanuatu, and thus may promote speciation in this island system.

This project is the first archipelago-wide study of intra-archipelago genetic variation for any vertebrate or invertebrate species within Vanuatu, and the insights generated by this study will be broadly applicable throughout the islands of the Pacific, an area with high biodiversity (Mittermeier et al. 1998a; Mittermeier et al. 1998b). The patterns of differentiation among islands provide important information regarding the role of island geologic history in driving speciation and enable inferences to be made regarding evolutionary processes during the early stages of a species radiation. Due to the recent emergence history of Vanuatu, the patterns

generated by evolutionary processes are not confounded by millions of years of evolutionary history, and can be uncovered using population genetic techniques.

In this dissertation chapter, I test seven specific hypotheses regarding the history of *E. sanfordi* in Vanuatu using mitochondrial DNA sequence data:

Hypothesis 1: Population structure in *E. sanfordi* is concordant with island formation and geologic history.

H_O: Genetic structure will reflect the three island belts. *Emoia sanfordi* populations will be more closely related to populations on other islands that formed as a result of the same period of volcanism than to populations from islands associated with a different volcanic origin.

H_A: Genetic structure will not be associated with the three periods of volcanism.

Hypothesis 2: Lowered sea levels and increased connectivity among islands will be reflected in the genetic structure of *Emoia sanfordi*.

H_O: Islands that were connected during lowered sea levels (such as Maewo and Pentecost) will show more admixtures of haplotypes reflected by comparisons of F_{ST} with each other than with islands that have no history of previous connections. Additionally, islands that were less isolated from each other historically as a result of sea level change will show less differentiation than those that have always been isolated.

H_A: Genetic structure will not reflect changes in sea level or island connectivity.

Hypothesis 3: Island populations are relatively isolated from each other, due to the ocean barrier separating them. These island populations this have a low degree of connectivity and occasional dispersal among islands drives the pattern of genetic variation.

H_O: Geographic distance and genetic divergence will be correlated for populations of *E. sanfordi*.

H_A: A pattern of isolation-by-distance will not be recovered.

Hypothesis 4: Genetic diversity in *E. sanfordi* is a result of accumulation of variation within isolated populations over time.

H_O: Older islands will have greater haplotype diversity and genetic diversity than younger islands.

H_A: Older islands will not have greater haplotype diversity and genetic diversity than younger islands.

Hypothesis 5: Populations of *E. sanfordi* on larger islands have more opportunity for intra-island differentiation than populations on smaller islands, due to the greater ecological opportunities present on larger islands.

H_O: Larger islands will have greater haplotype diversity and genetic diversity than younger islands.

H_A: Larger islands will not have greater haplotype diversity and genetic diversity than younger islands.

Hypothesis 6: Barriers to gene flow (such as high mountain ranges) on larger, more mountainous islands may have caused some populations to be isolated.

H_O: Islands with large mountain ranges will show a phylogeographic break concordant with the suggested barrier.

H_A: Islands with large mountain ranges will not show a phylogeographic break concordant with the suggested barrier.

Hypothesis 7: Small or isolated populations contribute significantly to genetic diversity and peripheral isolates are important in speciation and/or adaptation to new environments.

H_O: Small and/or isolated populations will have high genetic diversity or unique haplotypes.

H_A: Small and/or isolated populations will not have high genetic diversity or unique

haplotypes, but rather will represent a component of the diversity found on larger, less isolated islands.

MATERIALS AND METHODS

Sampling

Thirty-one sites on 13 islands were sampled for *Emoia sanfordi*, and localities included the northernmost and southernmost range limits of the species (Fig. 5.3). All major islands in the range of *E. sanfordi* were sampled, and multiple sites were included for several islands to assess the amount of genetic structure within islands. I collected *E. sanfordi* by hand and other methods (Hamilton et al. 2007) during four field seasons from June to October 2001, 2002, 2004, and 2005. Liver tissue or muscle tissue was collected from lizards and stored in 95% ETOH, and a subset of individuals from each site was collected as voucher specimens.

Molecular Data Collection

Samples from 270 *E. sanfordi* were included in this study (Table 5.1, Fig. 5.3). DNA was isolated from either muscle or liver tissues using either a Qiagen DNA Extraction kit following manufacturer instructions, or using the standard method of proteinase K digestion in lysis buffer followed by salt extraction (Aljanabi and Martinez 1997).

I used PCR to amplify 1054 aligned bases of double-stranded mitochondrial DNA products (378 bp of Cytb and 676 bp of Nd2) using the primers listed in Table 5.2. PCR was carried out in Omn-E or MJ PTC-200 thermal cyclers with the following conditions: (1) one cycle at 94°C for 2 min., 45 seconds at 48-56°C, and 72°C for either 1 min. or 1 min. and 20 seconds; (2) 34 cycles at 94°C for 2 min., 45 seconds at 48-56°C, and 72°C for either 1 min. or 1 min. and 20 seconds; (3) one cycle at 72°C for 6 min. A small number of samples were amplified under the following thermal cycler conditions: (1) one cycle at 94°C for 3 min. and 30 seconds, 50°C for 30 seconds, and 72°C for 1 min; (2) 44 cycles at 94°C for 30 seconds, 50°C

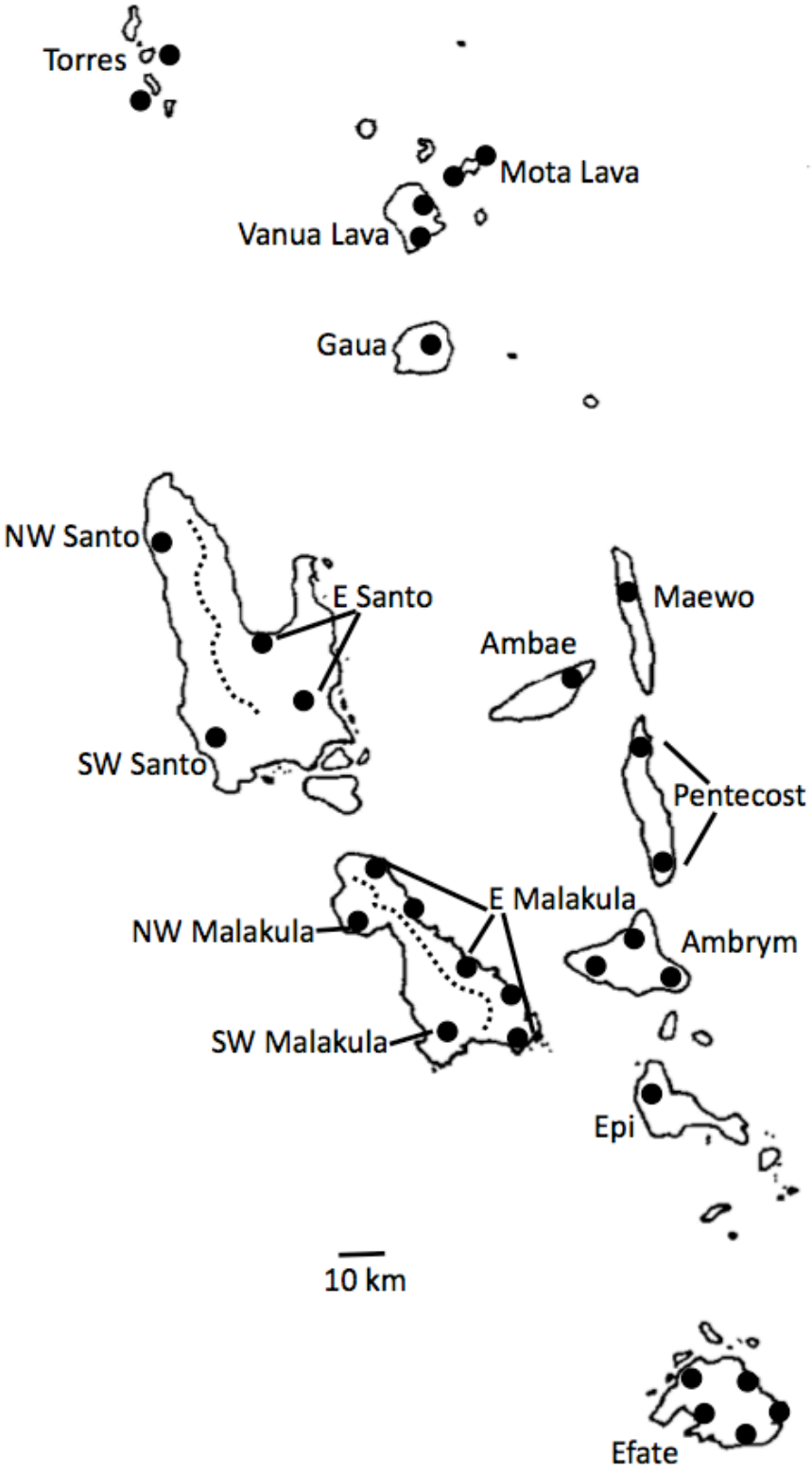


Figure. 5.3. Distribution of *Emoia sanfordi* in the Vanuatu Archipelago. Sampling locations are indicated with black dots. Groups of sampling localities that represent populations are indicated adjacent to islands. Mountain ranges bisecting the two largest islands (Malakula and Espiritu Santo) are indicated with dotted lines.

Table 5.1. Specimen numbers for *Emoia sanfordi* included in this study. Field collection abbreviations are as follows: CCA, Christopher C. Austin; AMH, Alison M. Hamilton, A, Steven Donellan. All CCA and AMH specimens were collected by Alison Hamilton as part of the research for this dissertation and are deposited at the Louisiana State University Museum of Natural Science.

Locality	Field Id.
Ambae	CCA 6008, 6011, 6022, 6027, 6031, 6058, 6069-70, 6072, 6074-75, 6078-79
Ambrym	
Ranon	CCA 7075, 7088-89, 7092, 7094, 7096-97, 7099, 7101, 7103-04
Penapo	CCA 6959, 6974-76
Craig Cove	CCA 6988, 6994-97, 7035
Efate	CCA 6415
Eton	AMH 004, 009, 010
Pango	CCA 6298, 6299
Epau	CCA 6318-19, 6321-23, 6327, 6331-32
Tanolilu	CCA 6357
MeleMat	CCA 6740
Epi	CCA 6909, 6920, 6922, 6927-28, 6933, 6940-41, 6943-49
Gaua	AMH 150-52, 155, 157-58, 160, 161, 172-75, 177-79, 181-82, 184, 186-88
Maewo	CCA 6097, 6109, 6117, 6119
Malakula	
Lavalsal	CCA 7500, 7512-13, 7517-18, 7527-29, 7532-33
Lakatoro	CCA 6236, 6241-51, 6253-55
Asurak	CCA 6848, 6853, 6869-70
Port Sandwich	A01, A09, A10, A11, A12
Wiawi	CCA 6801-02, 6808-11, 6815-17, 6819-20
Wintua	CCA 6267, 6269-81, 6285, 6287-93
Mota Lava	
Nerenigman	AMH 011, 015-16, 020, 029, 030
Telvet	CCA 7624, 7647, 7649-50, 7660, 7663, 7665, 7670, 7674-76, 7679, 7699
Santo	
Butmas	CCA 6160-62, 6164
Matantas	AMH 203, 206-10, 212, 219; CCA 6128, 6143, 6145-46
Lajmoli	CCA 6176, 6180, 6185-88, 6203-04, 6207-08
Tasariki	CCA 6218, 6220, 6222, 6224, 6227-29, 6231-33
Torres	
Loh	AMH 125-130
Tegua	AMH 110, 119, 121, 124, 131
Pentecost	
North	CCA 6596, 6617, 6622, 6635-36, 6638-42, 6644-47, 6649
South	7108-10, 7112-16, 1778-19, 7141, 7144, 7146, 7147
Vanua Lava	
Sola	AMH 039-41, 044, 048-50, 052-53, 055, 058, 060-61
Tenan	AMH 131, 143-145

Table 5.2. Primers used in this study.

Primer	Sequence (5' to 3')	Region	Source
H 15149	AAA CTG CAG CCC CTC AGA ATG ATA TT	Cytb	Kocher et al. 1989
L 14841	AAA AAG CTT CCA TCC AAC ATC TCA GG	Cytb	Kocher et al. 1989
M 120	TAA TAC ACC TAC TAT GAA AAA AYT T	Nd2	Austin lab
M 167	GCT GTY TGT GTY TGG TTT ADK CC	Nd2	Austin lab

for 30 seconds, and 72°C for 1 min.; (3) one cycle at 72°C for 10 min. Each 25 μl reaction contained 15.4 μl sterile water, 2.5 μl 10x PCR buffer, 1.5 μl of 25 nM $MgCl_2$, 0.5 μl of 10 nM dntp mix, 1 μl of 10 pM/ μl forward and reverse primers, 0.1 μl of Taq polymerase (Sigma-Aldrich, St. Louis, MO), and 3 μl of genomic DNA. All PCRS included a negative control (no DNA). Double-stranded PCR products were purified using the Ultra Clean Purification Kit (Mo Bio Laboratories, Solona Beach, CA) or ExoSAP-IT (USB Corporation, Cleveland, OH). PCR products were cycled sequenced using the original amplification primers and BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA). Sequenced products were cleaned up with CENTRI SEP Spin Columns and were visualized on an ABI 3100 sequencer. DNA sequences were edited with Sequencher 4.7, visually checked for accuracy, and aligned with Clustal X (Thompson et al. 1994).

Determination of Genetic Structure

Sequence data collected for Cytb for 269 individuals and Nd2 for 169 individuals were collapsed into haplotypes, and Arlequin v.3.11 (Schneider et al. 2000) was used to generate a minimum spanning tree, representing the distribution and frequency of haplotypes for each mitochondrial region. To determine the amount of genetic differentiation, F_{ST} values were calculated among all populations using Arlequin v.3.11 (Schneider et al. 2000).

To test specific hypotheses regarding the geographic structure of genetic variation with *E. sanfordi*, AMOVA were conducted using Arlequin v.3.11. Two analyses were performed for the Cytb and Nd2 datasets. The first analysis examined the partitioning of genetic structure by island formation, and included three 'populations': (1) the western belt islands of Santo, Malakula, and the Torres group; (2) the eastern belt islands of Pentecost and Maewo; and (3) the islands of the central belt including Maewo, Ambae, Ambrym, Epi, Efate, Gaua, Mota Lava, and Vanua Lava. A second analysis examined the partitioning of genetic structure associated with

historical changes in sea levels and connectivity among islands, and included three 'populations': (1) individuals from Maewo and Pentecost, as these islands were connected during lowered sea levels; (2) individuals from Malakula and Santo, as these islands may have been connected during lower sea levels, but certainly were more closely linked when sea levels fell; and (3) Ambrym and Epi, due to a closer historical connection.

To test the hypothesis that genetic variation is significantly correlated with geographic distance, I performed Mantel matrix regressions with Isolation By Distance Web Service v3.15 (Jensen et al. 2005; Bohonak 2002). I calculated a genetic distance matrix of all pairwise comparisons among populations from F_{ST} values computed in Arlequin v.3.11. Geographic coordinates from field collections of *E. sanfordi* were used to construct a matrix of geographic distances among populations using the Geographic Distance Matrix Generator (v.1.2.2), available through the Center for Biodiversity and Conservation at the American Museum of Natural History (http://biodiversityinformatics.amnh.org/open_source/gdmg). As I was interested in distances among populations, median geographic coordinates from all sampling sites were used for each population.

Genetic Diversity Measures

Population demographic data were calculated for each island using Arlequin v.3.11 (Schneider et al. 2000). Several measures of diversity were calculated for each island, including the number of haplotypes, nucleotide diversity, and mean number of pairwise differences between populations (Table 5.3). Genetic diversity measures were calculated for islands as opposed to populations as factors such as island size, habitat diversity, and island age (or length of population history) are likely to influence the genetic diversity. Comparing these measures of diversity between islands, rather than between populations on islands, enables an examination of the role of these historic and biotic factors on the amount of genetic diversity maintained and generated on oceanic islands

of varying ages, sizes, etc. Measures of genetic diversity were regressed against total island size (km^2), maximum island elevation (which I am considering to be a rough proxy for habitat diversity as oceanic islands with little change in elevation are likely to have fewer habitats), and age of most recent, continual emergence for each island. I use the length of time the island has been continually emergent as opposed to island age, as this is the measure of evolutionary time relevant to differentiation for populations of terrestrial organisms.

RESULTS

Patterns of Intra-archipelago Genetic Differentiation

There is significant genetic structure among populations recovered from Cytb and Nd2. A significant isolation-by-distance relationship was found for Nd2 (R^2=0.4209, P=0.0012) and for Cytb (R^2=0.4069, P=0.0024). A noticeable phylogeographic break occurs between the northern islands of Gaua, Mota Lava, Vanua Lava, and the Torres Group and the central and southern islands of Vanuatu within both Cytb (Fig. 5.4) and Nd2 (Fig. 5.5). The average pairwise distance between the northern and southern populations averages approximately 2% for each mitochondrial region and the island of Maewo is allied genetically with the northern islands despite its location in central Vanuatu. One common Cytb haplotype and four more rare haplotypes are distributed throughout the northern islands; in contrast there are several relatively common Nd2 haplotypes in these islands. There is not much genetic differentiation (pairwise distances range from 0% to 0.1%) among populations of *E. sanfordi* in the northern islands, all members of the most recently emergent central belt. None of the Cytb or Nd2 northern haplotypes was recovered from central or southern Vanuatu (with the exception of Maewo).

There is high haplotype diversity in the southern and central islands of Vanuatu, with 52 Nd2 haplotypes and 33 Cytb haplotypes recovered from the eight islands sampled (Figs. 5.4,

5.5). Many haplotypes are shared among islands, with neighboring islands sharing more haplotypes than distant islands. A few distinct breaks in the distribution of haplotypes were found in both Cytb and Nd2. Populations from Lajmoli, a location in the northwestern region of Espiritu Santo (northwestern Santo) are genetically differentiated from the other populations on this island (southwestern Santo and eastern Santo). This Lajmoli population is located on the western side of a mountain range that extends southward along the coast of the island. Two Cytb haplotypes (K and M) were sampled from this population (Fig. 5.4); neither haplotype was recovered from any other populations sampled, including the three other locations on the islands of Espiritu Santo. Likewise, six Nd2 haplotypes were recovered from Lajmoli (Fig. 5.5), and only one of these (haplotype D5) was found in another population (Eastern Santo).

Despite their geographic proximity, Maewo does not share either Cytb or Nd2 haplotypes with the islands of Pentecost or Ambae. Two Cytb haplotypes were sampled from Maewo, and these are both shared with the northern islands. Similarly, the two Nd2 haplotypes from the population on Maewo are likewise shared with the populations in northern Vanuatu (Fig. 5.5). Pentecost and Ambae share haplotypes with each other, and with the nearby islands of Epi, Ambrym, Malakula, and Santo. Like the population from northwestern Santo, the northwestern Malakula population appears to be genetically differentiated from the remainder of the populations sampled on this island (Fig. 5.4). A single Cytb haplotype was present in all ten individuals sampled from this site (haplotype C) and is unique to this population. Due to reduced sampling for Nd2 from this population, all the individuals from Malakula were analyzed as a single population for Nd2, so whether this differentiation is also present at Nd2 is not known.

In general, pairwise differences for F_{ST} values between populations were high, indicating a large amount of genetic structure among populations. Results from F_{ST} values suggest patterns

Table 5.3. Population diversity statistics generated using Arlequin.

	N	Hap	Gene Diversity	Nucleotide Diversity	Mean Pairwise Differences
Cytb					
Maewo	4	2	0.500 ± 0.27	0.007 ± 0.005	2.500 ± 1.686
Pentecost	25	4	0.617 ± 0.08	0.003 ± 0.002	1.207 ± 0.797
Efate	16	3	0.542 ± 0.10	0.015 ± 0.009	5.750 ± 2.905
Epi	12	4	0.455 ± 0.17	0.002 ± 0.002	0.803 ± 0.621
Gaua	19	2	0.199 ± 0.11	0.001 ± 0.001	0.199 ± 0.259
Santo	47	17	0.804 ± 0.06	0.015 ± 0.008	5.611 ± 2.742
Torres	10	2	0.356 ± 0.16	0.001 ± 0.001	0.356 ± 0.375
Vanua Lava	16	4	0.350 ± 0.15	0.002 ± 0.002	0.750 ± 0.583
Malakula	64	9	0.664 ± 0.05	0.012 ± 0.007	4.498 ± 2.244
Mota Lava	18	2	0.209 ± 0.12	0.003 ± 0.003	1.254 ± 0.830
Ambrym	22	3	0.481 ± 0.09	0.004 ± 0.003	1.455 ± 0.918
Ambae	13	3	0.295 ± 0.16	0.001 ± 0.001	2.500 ± 1.686
Nd2					
Maewo	4	2	0.500 ± 0.27	0.011 ± 0.008	7.500 ± 4.441
Pentecost	14	5	0.725 ± 0.09	0.006 ± 0.004	3.890 ± 2.076
Efate	10	4	0.644 ± 0.15	0.018 ± 0.010	12.289 ± 6.071
Epi	10	4	0.533 ± 0.18	0.002 ± 0.001	1.022 ± 0.744
Gaua	18	6	0.628 ± 0.12	0.003 ± 0.002	2.307 ± 1.324
Santo	28	19	0.958 ± 0.02	0.001 ± 0.005	6.624 ± 3.224
Torres	11	2	0.182 ± 0.14	0.000 ± 0.000	0.182 ± 0.253
Vanua Lava	12	5	0.576 ± 0.16	0.001 ± 0.001	0.939 ± 0.692
Malakula	35	17	0.872 ± 0.04	0.011 ± 0.006	7.079 ± 3.404
Mota Lava	6	2	0.333 ± 0.22	0.001 ± 0.001	0.333 ± 0.380
Ambrym	8	2	0.536 ± 0.12	0.002 ± 0.002	1.607 ± 1.060
Ambae	11	3	0.346 ± 0.17	0.002 ± 0.001	1.091 ± 0.773

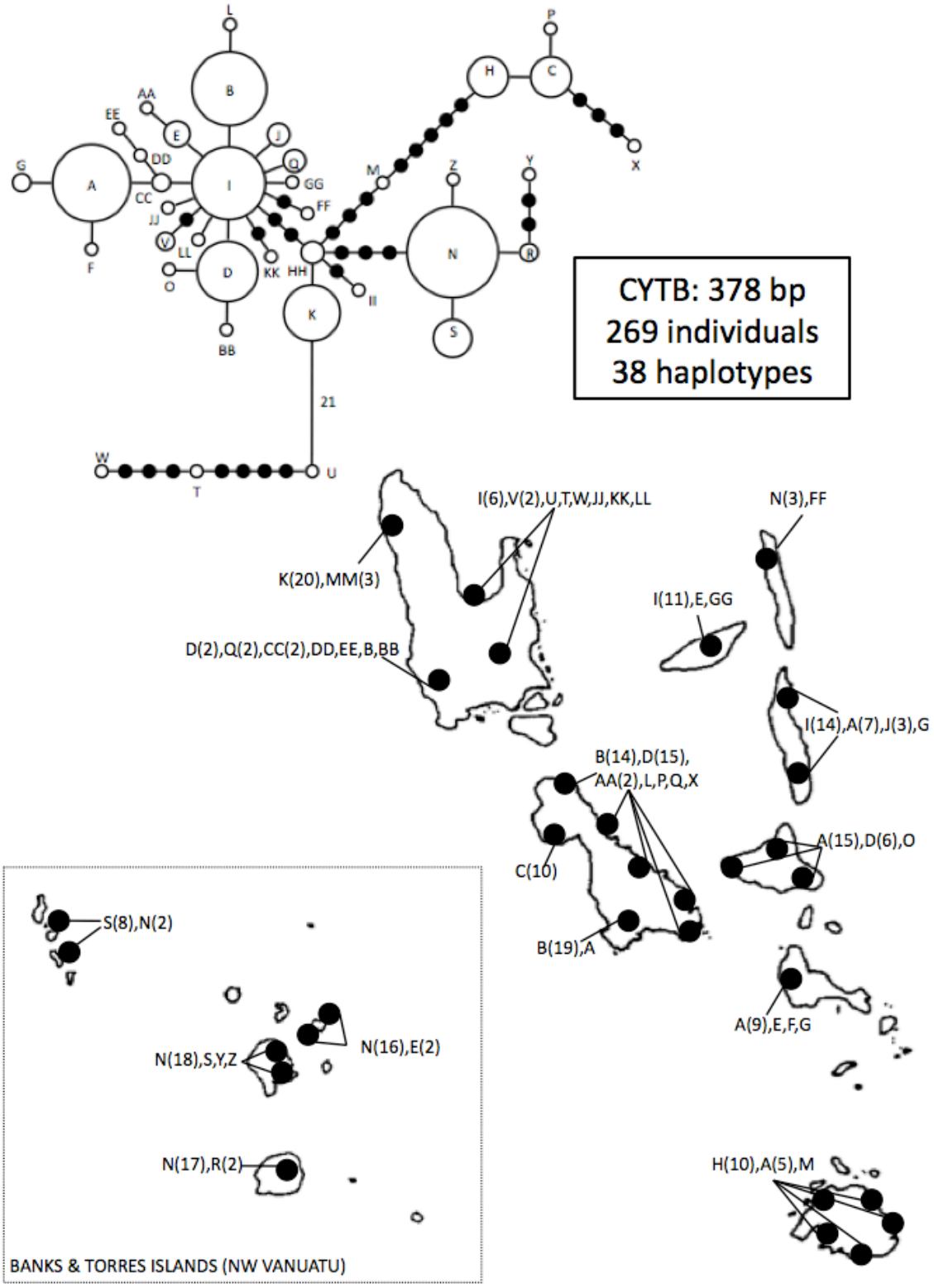


Figure 5.4. Haplotype network for a 378 bp fragment of Cytb for 269 individuals of *Emoia sanfordi*. Sampling locations and the corresponding populations are shown. Haplotypes recovered from each population are indicated. Number of individuals with each haplotype is indicated in parentheses; if no number is provided the haplotype was only recovered from a single individual in the population.

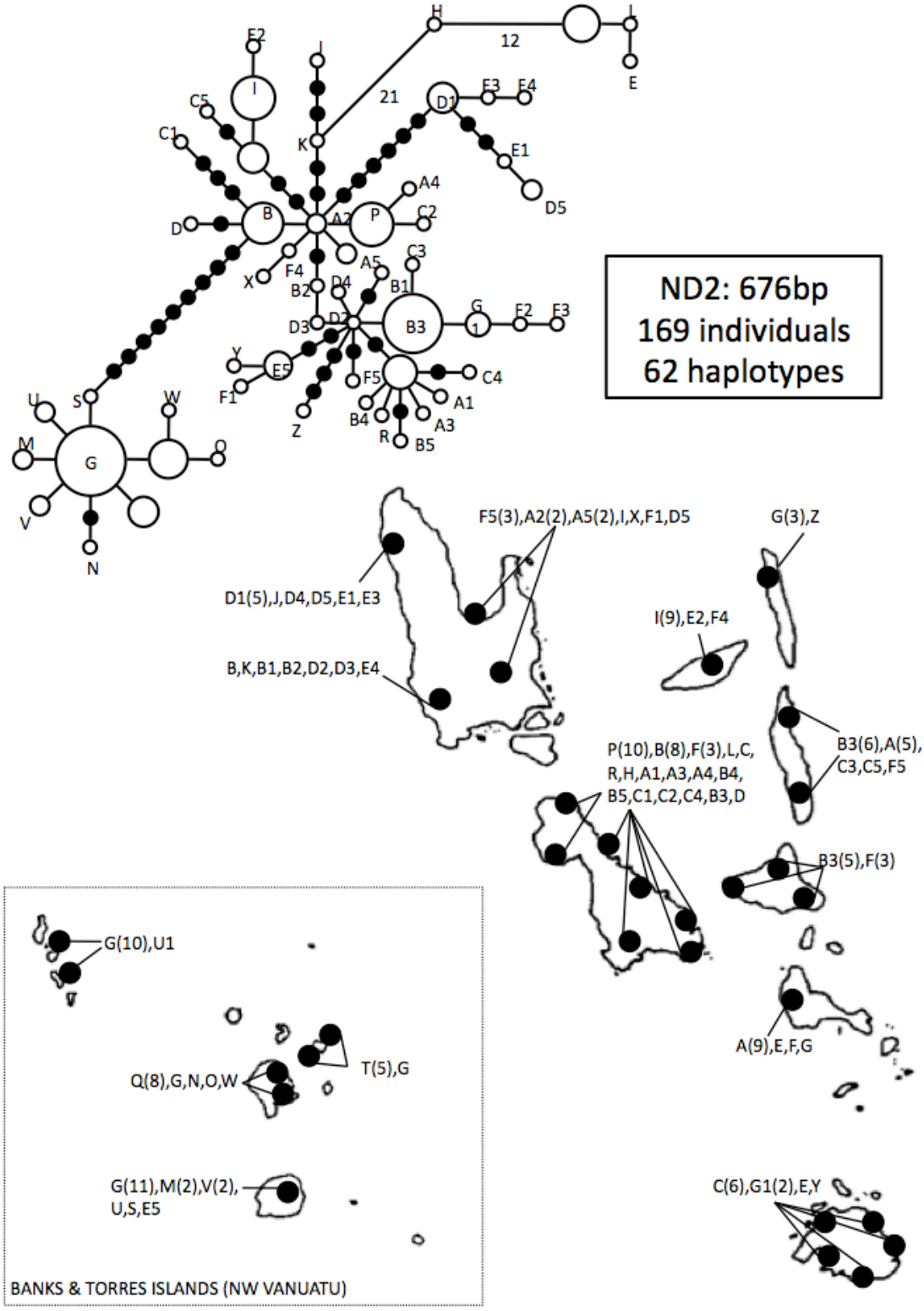


Figure 5.5 Haplotype network for a 676 bp fragment of Nd2 for 169 individual *Emoia sanfordi*. Sampling locations and the corresponding populations are shown. Haplotypes recovered from each population are indicated. Number of individuals with each haplotype is indicated in parentheses; if no number is provided the haplotype was only recoverd from a single individual in the population.

of gene flow that are concordant with the distribution of haplotypes among the islands (Figs. 5.6 and 5.7). Very low pairwise values for F_{ST} (many pairwise differences <0.1) were calculated from both Cytb and Nd2 data between pairs of populations in the northern islands. High pairwise differences for F_{ST} were found between the population from northwest Santo and all other populations for Cytb and Nd2. The population from northwestern Malakula also had large pairwise differences for F_{ST} for Cytb.

Period of volcanism, or timing of island origin, did not explain a significant amount of the genetic variation for *E. sanfordi* in Vanuatu (Hypothesis 1). In fact, none of the observed genetic variation was related to variation among groupings of populations associated with the three geologic belts (Table 5.4). AMOVA results indicate most of the Nd2 variation in the analysis was explained by variation among islands within the three geologic belts (72%), and that variation in Cytb was explained equally well by variation among islands within each geologic belt and within islands themselves (Table 5.4). Hypothesis 2 was also not supported by the results of an AMOVA, as little of the observed genetic variation (2.5% for Cytb and 3.89% for Nd2) is caused by the relationships among islands that were previously connected or had reduced dispersal distances during periods of lower sea level (Table 5.4). AMOVA results suggest that most of the observed variation is found within island populations.

Genetic Diversity

Both gene diversity and nucleotide diversity were high on Santo and Malakula, the two largest islands in the Vanuatu Archipelago (Fig. 5.8). Nucleotide diversity was high on Efate, and Pentecost has a large amount of gene diversity. In general, nucleotide diversity and gene diversity were found to be low on the small islands in the northern Vanuatu (Table 5.3). Islands in central Vanuatu, many of which have shared haplotypes, generally had moderate levels of both nucleotide diversity and gene diversity (Fig. 5.8).

A weak, positive relationship was observed between island area and gene diversity (Fig. 5.9), with island area explaining 57% of the variation in gene diversity for Nd2 and 62% of the variation in gene diversity for Cytb. The relationship between island area and nucleotide diversity was also positive, but weaker, as island area explains 58% of the variation in nucleotide diversity for Cytb, but only and 21% of the variation in gene diversity for Nd2. There was no was no relationship observed between the maximum elevation of an island and either gene diversity or nucleotide diversity (Fig. 5.9). Timing of island formation also did not appear to have an affect on genetic diversity (Fig. 5.9), as no relationship was observed between timing of island formation and gene diversity of nucleotide diversity.

DISCUSSION

The data presented in this chapter are the first broad examination of intra-archipelago genetic variation for a non-volant vertebrate species in the Vanuatu Archipelago. There is a high degree of genetic structure within *Emoia sanfordi* in Vanuatu, and this genetic structure is associated with geography. The distribution of haplotypes and genetic variation, as well as the amount of gene and nucleotide diversity from islands throughout the Vanuatu Archipelago were used to test seven specific hypotheses regarding the history of *E. sanfordi* in this island group.

1. Population structure in *E. sanfordi* is a result of island formation and geologic history.

The data do not provide support for this hypothesis, as genetic structure was not associated with the three periods of volcanism that formed the islands of Vanuatu. Although Santo and Malakula, both western belt islands associated with the earliest period of volcanism, share a large number of haplotypes with each other and show evidence (based on pairwise F_{ST} values) of gene flow, the connectivity between these islands does not appear to be a result of early colonization history associated with island formation. The results of the AMOVA indicated that the observed genetic variation was not a result of variation among islands associated with the distinct periods

Figure 5.6. Patterns of gene flow and genetic connectivity among populations of *E. sanfordi* on islands in Vanuatu based on mean pairwise F_{ST} values between populations from Cytb data. Significant breaks in the genetic structure of the species as suggested by very high mean pairwise F_{ST} values are indicated with dotted lines. The degree of gene flow is indicated by the thickness of the arrows connecting populations; thicker arrows represent high levels of gene flow. The shaded northern islands have such low mean pairwise F_{ST} values that they could not be distinguished from 0, and thus represent a single, panmictic population of *E. sanfordi*. Abbreviations: NW Malakula=northwestern Malakula, SW Santo=southwestern Santo, E Santo=eastern Santo, NW Santo=northwestern Santo.

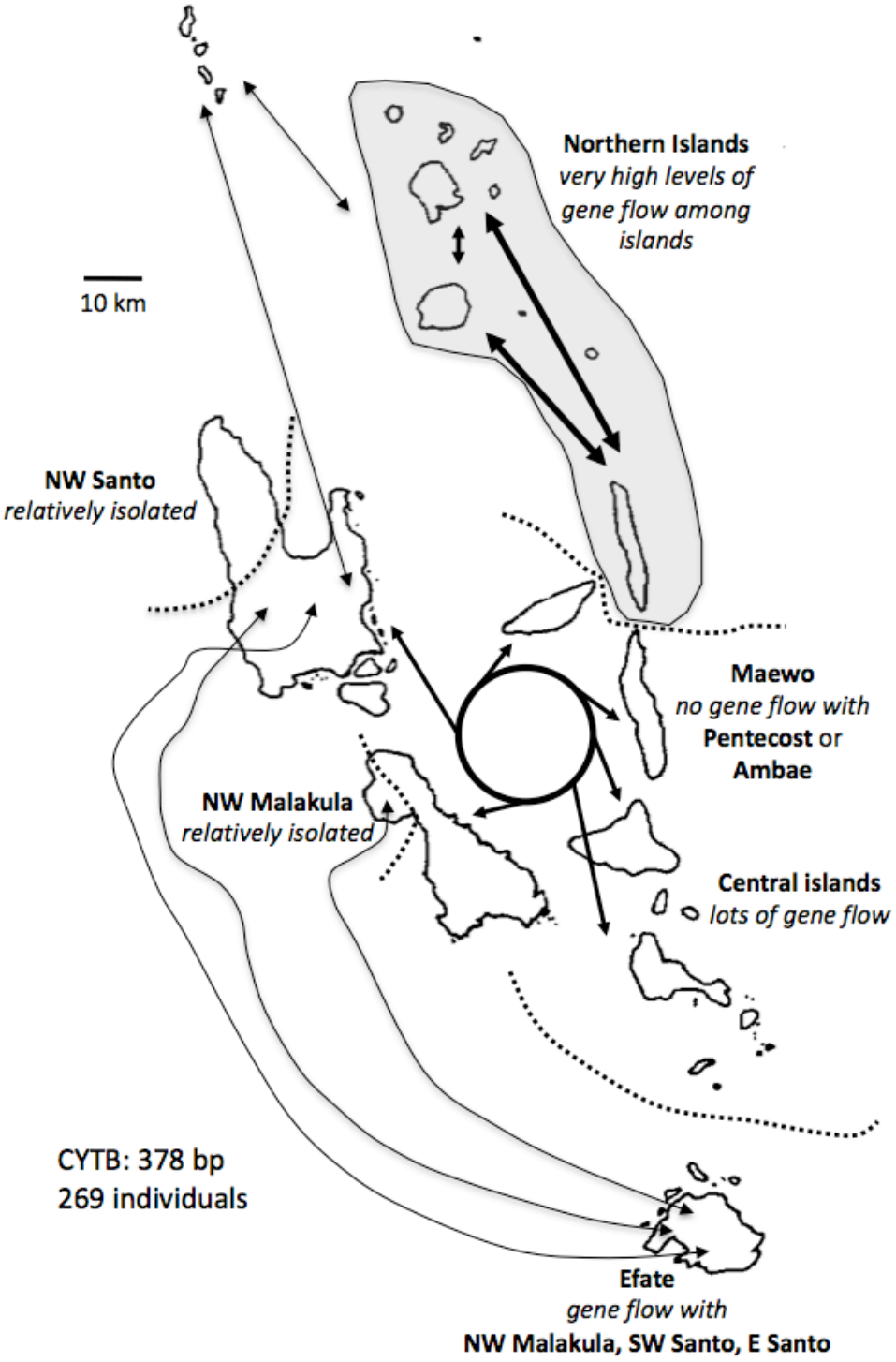

Northern Islands
very high levels of gene flow among islands
10 km
NW Santo
relatively isolated
Maewo
no gene flow with Pentecost or Ambae
NW Malakula
relatively isolated
Central islands
lots of gene flow
CYTB: 378 bp
269 individuals
Efate
gene flow with
NW Malakula, SW Santo, E Santo

Figure 5.7. Gene flow and genetic connectivity among populations of *E. sanfordi* on islands in Vanuatu based on mean pairwise F_{ST} values between populations from Nd2 data. Significant breaks in the genetic structure of the species suggested by very high mean pairwise F_{ST} values are indicated with dotted lines. The degree of gene flow is indicated by the thickness of the arrows connecting populations; thicker arrows represent high levels of gene flow. The shaded northern islands have such low mean pairwise F_{ST} values that they could not be distinguished from 0, and thus represent a single, panmictic population of *E. sanfordi*. Likewise, high amounts of gene flow between Malakula, Eastern Santo, and Southwestern Santo are indicated by a circle. Abbreviations: NW Malakula=northwestern Malakula, SW Santo=southwestern Santo, E Santo=eastern Santo, NW Santo=northwestern Santo.

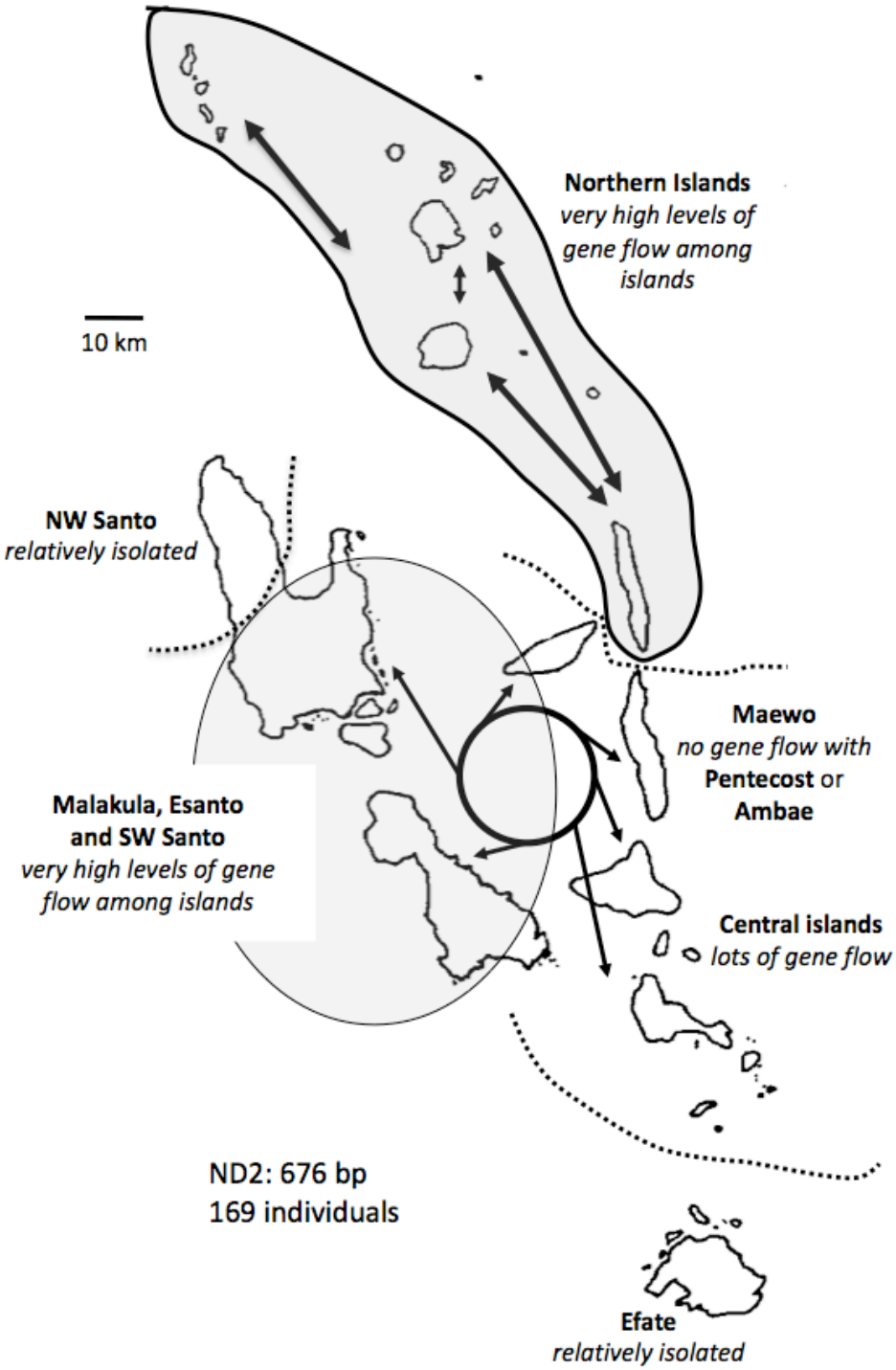

Northern Islands
very high levels of gene flow among islands
10 km
NW Santo
relatively isolated
Maewo
no gene flow with Pentecost or Ambae
Malakula, Esanto and SW Santo
very high levels of gene flow among islands
Central islands
lots of gene flow
ND2: 676 bp
169 individuals
Efate
relatively isolated

Table 5.4. Results of AMOVA used to test specific hypotheses about the history of *Emoia sanfordi* in the Vanuatu Archipelago.

Comparison	Variation explained	F	P
Hypothesis 1: *Episode of volcanism*			
Among groups: Nd2	-12.53	-.1253	.72630
Among groups: Cytb	-9.86	-.0986	.70577
Among populations (within groups): Nd2	72.18	.6415	<.00001*
Among populations (within groups): Cytb	58.55	.5329	<.00001*
Within populations: Nd2	40.35	.5956	<.00001*
Within populations: Cytb	51.32	.4868	<.00001*
Hypothesis 2: *Island connectivity and sea-level change*			
Among groups: Nd2	2.5	.0250	.05670
Among groups: Cytb	3.89	.0389	.35386
Among populations (within groups): Nd2	23.03	.2363	<.00001*
Among populations (within groups): Cytb	25.41	.2643	<.00001*
Within populations: Nd2	74.47	.2554	<.00001*
Within populations: Cytb	70.70	.2930	<.00001*

Figure 5.8. Geographic distribution of population level genetic diversity for *E. sanfordi* within Vanuatu. Levels of nucleotide diversity (left) and gene diversity are shown for each population. Populations with a single color circle are those for which Cytb and Nd2 diversity were the same (i.e., both high values). Populations with a divided circle indicate that the level of diversity observed differed between Cytb and Nd2. For these populations, the left half of the circle represents Cytb data and the right side of the circle represents Nd2 data. Diversity statistics for all populations are provided in Table 5.3.

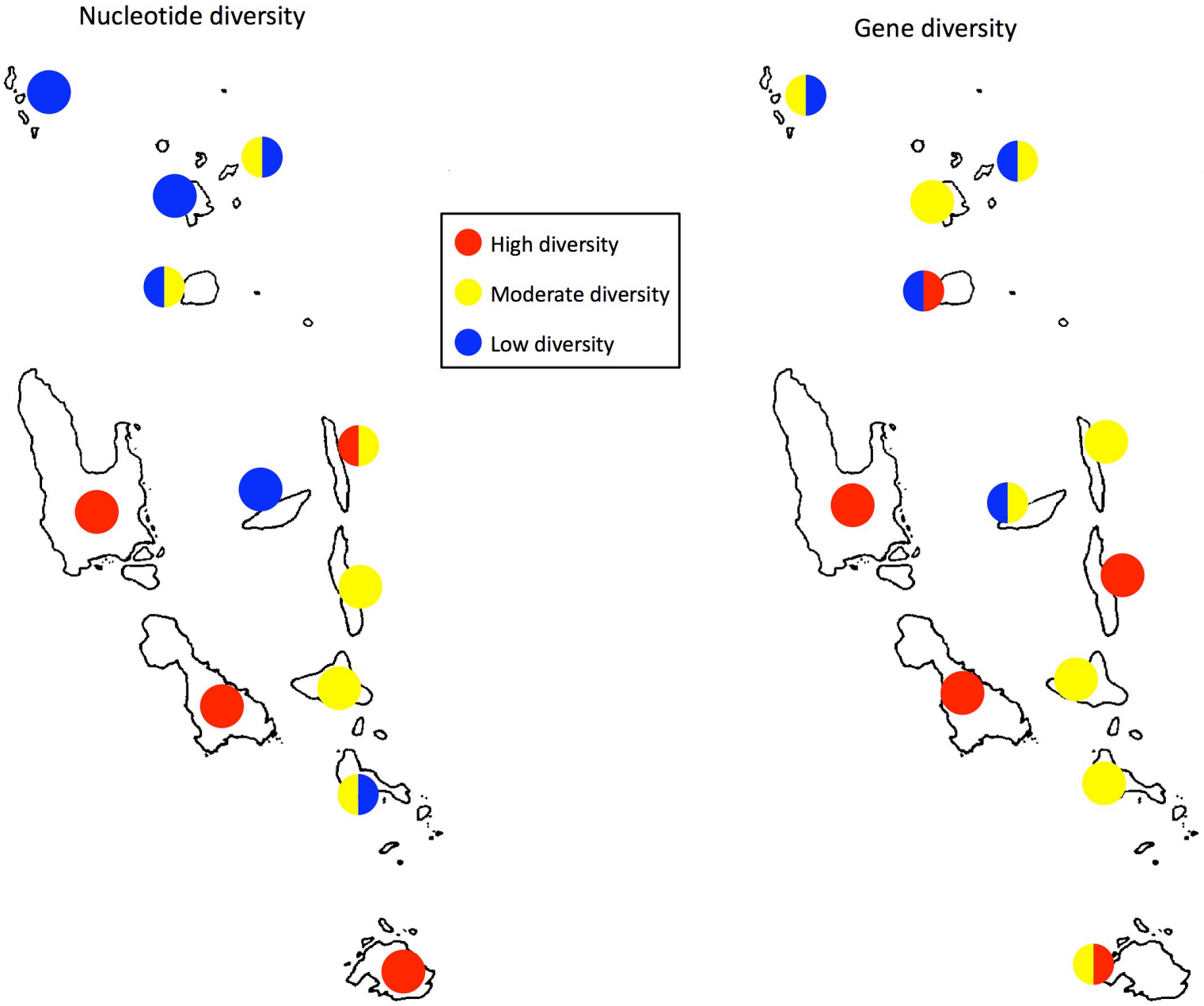
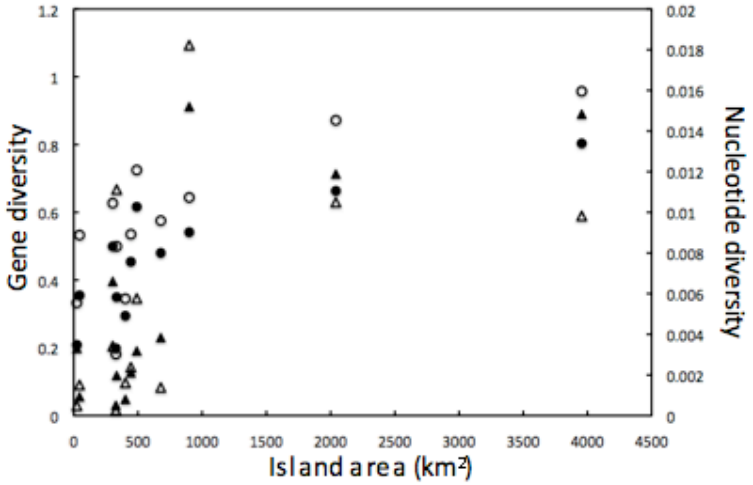
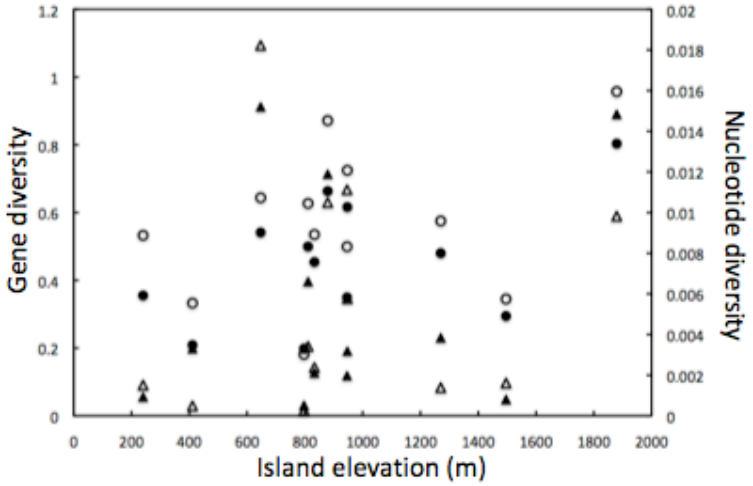
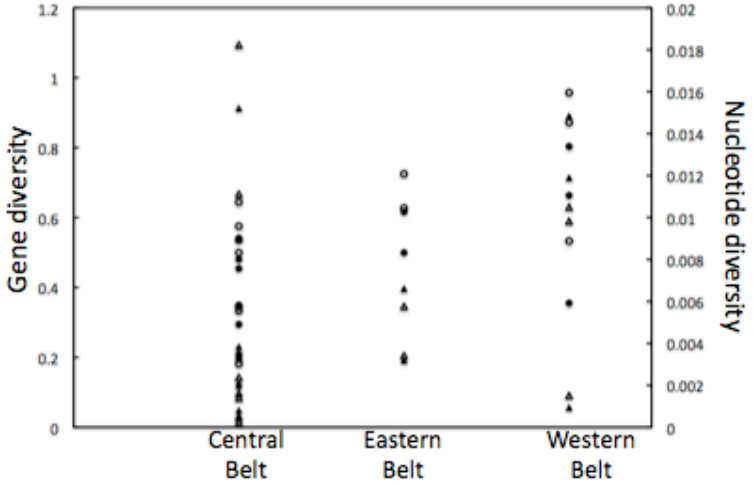

Nucleotide diversity
Gene diversity
High diversity
Moderate diversity
Low diversity

Figure 5.9. Relationship between measured of population level genetic diversity for *E. sanfordi* and island characteristics that may influence diversity: island area, island elevation, and island geologic history. Circles are used to represent data for gene diversity (open circle Nd2, closed circle Cytb), and triangles are used to represent nucleotide diversity (open triangle Nd2, closed triangle Cytb). A weak, positive relationship is observed between island area and both gene diversity and nucleotide diversity, but no relationship is observed between either measured of genetic diversity and either island elevation, or timing of island formation.


Gene diversity
Nucleotide diversity
Island area (km²)
0
500
1000
1500
2000
2500
3000
3500
4000
4500


Gene diversity
Nucleotide diversity
Island elevation (m)
0
200
400
600
800
1000
1200
1400
1600
1800
2000


Gene diversity
Nucleotide diversity
Central Belt
Eastern Belt
Western Belt

of volcanism that resulted in island formation. Additionally, the two eastern belt islands of Pentecost and Maewo have no signature of a shared history, and are highly differentiated from each other with respect to the distribution of haplotypes. Pairwise F_{ST} values for these two islands do not suggest frequent gene flow between them.

2. Lowered sea levels and increased connectivity among islands will be reflected in the genetic structure of *E. sanfordi*.

The distribution of haplotypes among islands does not support this hypothesis. Islands known to have a land connection during lower sea levels, such as Maewo and Pentecost, do not share haplotypes as was predicted, but are highly differentiated. Additionally, AMOVA results indicate that the observed genetic variation was not a result of variation among groups of islands that experienced increased connectivity during the last glacial maximum.

3. Island populations are relatively isolated from each other, due to the ocean barrier separating them. These island populations have a low degree of connectivity and occasional dispersal among islands drives the pattern of genetic variation.

A pattern of isolation-by-distance was recovered for both Cytb and Nd2, indicating that a correlation exists between genetic and geographic distance for *E. sanfordi*. This distribution of genetic variation suggests that dispersal among islands is likely responsible, at least to some extent, for the pattern of genetic variation observed. However, the distribution of haplotype data indicates that some island populations appear more isolated than others, and the relationship between shared haplotypes and geographic distance is not always obvious. Pairwise FST values also suggest that the amount of gene flow occurring among islands is highly variable, and is not explained solely by the straight-line geographic distance among islands.

4. Genetic diversity in *E. sanfordi* is a result of accumulation of variation within isolated populations over time.

A strong relationship between island age and genetic diversity was not found for *E. sanfordi*, indicating that haplotype diversity is not higher on the oldest islands. Accumulation of genetic diversity on islands may still be an important driver of genetic diversity, but the signal of historical accumulation may have been erased by ongoing gene flow within Vanuatu.

5. Colonizing populations of *E. sanfordi* on larger islands have more opportunity for intra-island differentiation than populations on smaller islands, due to the greater ecological opportunities present on larger islands.

The two largest islands in Vanuatu are Santo and Malakula, both of which have high gene diversity, nucleotide diversity, and haplotype diversity. In addition to this large amount of diversity, each of these islands has a population that is highly differentiated from the remainder of the populations on the island and elsewhere in the archipelago (Lajmoli in northwest Santo, and Wiawi on northwest Malakula). The potential role of island area in promoting differentiation in these islands, however, is confounded by the age of Malakula and Santo, the two oldest islands in the chain, and the presence of significant dispersal barriers (large mountain ranges).

6. Barriers to gene flow (such as high mountain ranges) on larger, more mountainous islands may have caused some populations to be isolated.

Mountain ranges on both Santo and Malakula are associated with breaks in the distribution of haplotypes across these islands. On both islands, populations of either side of the mountain range share few, if any haplotypes, and pairwise FST values are much higher between these two northwestern populations (Lajmoli and Wiawi) and populations occurring on the other side of these mountain ranges on Santo and Malakula.

Although the data provide evidence of phylogeographic breaks on Santo and Malakula, it is not clear if these potential barriers have driven the observed differentiation within islands. It is also possible that these divergent lineages result from secondary colonization of these islands by *E. sanfordi*, and that subsequent population expansion and introgression of secondary colonists into the main population has been prevented by a dispersal barrier (i.e., a mountain range).

7. Small or isolated populations contribute significantly to genetic diversity and peripheral isolates are important in speciation and/or adaptation to new environments.

Small islands, and clusters of relatively isolated islands such as the northern islands of Vanuatu, contain unique and divergent haplotypes. In general, gene diversity and nucleotide diversity were lower on small islands and on isolated islands; these islands, however, did not simply represent a subset of the diversity recovered elsewhere, but contained some haplotypes that were genetically distinct from other islands. The data presented in this study do not address the potential role of this genetic variation in enabling populations to adapt to novel environments, or in the process of speciation. From a conservation perspective, it is significant to note that large islands, although they have high levels of diversity, do not represent the extent of the genetic variation within *E. sanfordi*.

The results of this study are in sharp contrast to previous work on three species of birds (a rail, a dove, and a fantail) in Vanuatu. For all three species, no geographic structure was recovered in the genetic variation detected at CO1, and there was no clustering of haplotypes by island (Kirchman and Franklin 2007). Pairwise FST values from all three species were low: near 0 in the rail and the dove and <0.35 for the fantail (Kirchman and Franklin 2007). Why the pattern of genetic variation in Vanuatu should differ so dramatically between birds and lizards is puzzling. It is possible that the seemingly incongruent results of this study and that of Kirchman and Franklin (2007) is simply a result of differences in sampling designs. Overall sample sized

were much lower in Kirchman and Franklin (2007) with only 21 individuals of the rail and dove species, respectively, and 23 fantails sampled from Vanuatu. Additionally, the sampling was limited geographically, with individuals included in this study from only four islands (Efate, Santo, Malakula, and Vanua Lava).

The low FST values and high level of shared haplotypes among sites for these bird species from the eastern regions of Santo and Malakula is a pattern similar to that found for E. sanfordi from the eastern populations of these two islands. The unique haplotypes and evidence for lack of connectivity (high FST values) that we report from these islands are from populations in the northwestern areas of Santo and Malakula, areas not sampled by Kirchman and Franklin (2007). The large difference in the overall level of pairwise FST values and θ reported previously for birds and FST values and measures of population level genetic diversity I present for *E. sanfordi*, however, remains unexplained.

An obviously possible cause for the lack of concordance between these results and those of Kirchman and Franklin (2007) is the difference in vagility between birds and lizards, resulting in differences in isolation of populations of the two taxonomic groups. This is certainly likely to be the case, but whether this difference in vagility would be enough to result in such different patterns of genetic variation is questionable. Another important difference between *E. sanfordi* and the bird species studied by Kirchman and Franklin (2007) is the distribution of the taxa in question. All three species of birds have relative broad distributions, extending at least throughout most of Oceania (Kirchman and Franklin 2007), whereas *E. sanfordi* is endemic to this archipelago, and is part of a lineage that has apparently undergone multiple speciation events within these islands (Hamilton et al., unpublished data; Chapter 4 this dissertation).

A multilocus approach may help elucidate the history of *E. sanfordi* in Vanuatu and the role of geology, isolation, and environmental factors in shaping the genetic variation of *E.*

sanfordi. Understanding the factors that have lead to such high levels of genetic diversity and population-level differentiation on a small spatial scale will provide insight into the mechanisms of speciation at work in oceanic island systems.

CHAPTER 6: CONCLUSIONS

The Species-Area Relationship does not consider all the relevant, and perhaps most important, components of biodiversity such as speciation, which is crucial to the evolution of island biotas. Because of the isolated nature of oceanic Pacific islands, speciation is essential in the development of island faunas. For island groups in the southwestern Pacific, degree of endemism in an island group increased as the size of the largest island in the group increased; the size of the largest island accounted for 79% of the observed variation in the level of endemism. The relationship between the proportion of an archipelago that consisted of islands ≥ 3,000 km^2 and archipelago endemism was also positive. Archipelagos in which a greater proportion of the total area was made up of larger islands (i.e. the Solomon Islands and New Caledonia) had higher endemism, and those with large numbers of small islands and no really large islands (i.e. Tonga and the Loyalty Islands) had lower levels of endemism.

The data presented in this dissertation are congruent with the idea that larger islands should have greater endemism, and provide partial support for the predictions that endemism should be greatest on larger, isolated islands, and that an insular size threshold exists above which speciation becomes the significant contributor to species diversity. These data do not provide support for the relationship between endemism and isolation alone. Island size, rather than isolation, seems to be more important for lizards and mammals, perhaps due to their intermediate vagility.

Overall, I did not find evidence to support the suggestion that Vanuatu has a depauperate fauna. Lizard diversity in the Vanuatu Archipelago, and all other archipelagos in this study, meets the pattern predicted by the SAR. When the archipelagos were compared with respect to their ability to generate diversity through speciation as opposed to immigration, Vanuatu has the

expected rate of endemism. Furthermore, the ratio of both number of species and endemic species to the amount of time since emergence for Vanuatu is almost twice that for all other island groups considered in this study. The development of high species richness over a short geologic timescale as seen in the Vanuatu Archipelago does not support the suggestion that the lizard fauna is depauperate. Overall, the lizard fauna of Vanuatu appears to fit the expectation for diversity relative to other OMA archipelagos.

Differentiating between human-mediated dispersal and waif over-water dispersal is difficult, especially in the islands of Oceania due to the complex and recent history of human migrations in the region. The phylogenetic relationships among species of *Emoia* examined in this dissertation provide support for both the human-mediated dispersal hypothesis and the possibility that the Rarotonga population dispersed by natural means and thus represents the sole species of reptile native to the Cook Islands. The population on Rarotonga forms a monophyletic group that is well differentiated from other species in the recovered topology. In contrast, the topology of the phylogeny shows very low genetic variation (only 0.3%) within the clade from Rarotonga, a pattern more consistent with a history of human-mediated dispersal. The distinctiveness of the population of *Emoia* on Rarotonga coupled with such a low level of variation within the population is confusing, as the two sets of data do not support a single hypothesis but rather appear to contradict each other. Comparison of population level genetic diversity measures for the Rarotonga population and the simulated populations of *E. aneityumensis* generated using a statistical resampling approach provide support for a human-mediated introduction to Rarotonga. In all 485 comparisons between equal-sized populations of *E. aneityumensis* (endemic to the island of Aneityum, Vanuatu) and empirical data from Rarotonga, three measures of genetic diversity (π, θ_w, and haplotype diversity) were greater for the population of *E. aneityumensis* in every case and haplotype diversity was lower for the

population from Rarotonga than populations of six single island endemic species of *Emoia* from Vanuatu for data from Cytb, Nd4, and CO1. In combination, these results suggest that the amount of genetic diversity that we expect to observe in a species of this lineage of *Emoia* that is endemic to an oceanic island in the Pacific is much greater than the level of genetic variation present in the population from Rarotonga.

Monophyly of the *Emoia samoensis* group based on a combined mitochondrial and nuclear dataset suggests that this lineage of relatively large, primarily arboreal scincid lizards represent a radiation of species in the islands of the southwest Pacific Ocean, and the geographic distribution of these species suggests that this lineage has diversified on these remote islands, as all members of this lineage occur on oceanic islands in Oceania and Melanesia. The topology of the recovered phylogeny suggests a single invasion of the region by an ancestral taxon and a simple stepping stone model of colonization for the *Emoia samoensis* group in the Pacific.

We do not find evidence for sympatric speciation within this lineage. Only one pair of sister taxa are sympatric: *Emoia* B and *E. nigromarginata*. These two species are weakly differentiated with respect to body size, but this difference is not great even when genetic distance is accounted for. The strong relationship between body size and shape, particularly head shape, is the evolutionary pattern we would expect to recover in the absence of strong selection on morphology. The relationship between both measures of morphological distance (size and shape) with genetic distance is suggestive of the role of ecology in diversification in this species group. The increased morphological differentiation relative to time since speciation for sympatric taxa is suggestive of the role of ecology on the evolution of morphology in these taxa, especially in light of the evidence for morphological conservatism in *Emoia* and other Pacific scincid lizards. The combination of morphological stasis combined with the potential for rapid evolution of morphological traits, potentially as a result of divergent selection, has created

taxonomic confusion with respect to defining species boundaries among the *Emoia samoensis* group members has been difficult, but the data presented in this dissertation is an important step in understanding how species radiations arise and diversify.

Data presented in this dissertation are the first broad examination of intra-archipelago genetic variation for a non-volant vertebrate species in the Vanuatu Archipelago. There is a high degree of genetic structure within *Emoia sanfordi* in Vanuatu, and this genetic structure is associated with geography. Population structure in *E. sanfordi* is not a result of island formation and geologic history, and genetic structure is not associated with the three periods of volcanism that formed the islands of Vanuatu. Based on the distribution of haplotypes among islands, lowered sea levels and increased connectivity among islands is not reflected in the genetic structure of *E. sanfordi*. Islands known to have a land connection during lower sea levels, such as Maewo and Pentecost, do not share haplotypes as was predicted, but are highly differentiated. A pattern of isolation-by-distance was recovered for both Cytb and Nd2, indicating that a correlation exists between genetic and geographic distance for *E. sanfordi*. A strong relationship between island age and genetic diversity was not found for *E. sanfordi*, indicating that haplotype diversity is not higher on the oldest islands, and that genetic diversity within populations of this species are not simply a result of accumulation over time. The two largest islands in Vanuatu are Santo and Malakula, both of which have high gene diversity, nucleotide diversity, and haplotype diversity. In addition to this large amount of diversity, each of these islands has a population that is highly differentiated from the remainder of the populations on the island and elsewhere in the archipelago (Lajmoli in northwest Santo, and Wiawi on northwest Malakula).

Mountain ranges on both Santo and Malakula are associated with breaks in the distribution of haplotypes across these islands. Small islands, and clusters of relatively isolated

islands such as the northern islands of Vanuatu, contain unique and divergent haplotypes. In general, gene diversity and nucleotide diversity were lower on small islands and on isolated islands; these islands, however, did not simply represent a subset of the diversity recovered elsewhere, but contained some haplotypes that were genetically distinct from other islands. Understanding the factors that have lead to such high levels of genetic diversity and population-level differentiation on a small spatial scale will provide insight into the mechanisms of speciation at work in oceanic island systems.

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APPENDIX 1: SPECIES LISTS FOR ISLAND GROUPS INCLUDED IN CHAPTER 2

Table A. *Hemidactylus frenatus*, *H. garnotii,* and *Lepidodactylus lugubris* are considered introduced to all island groups included in this comparison and therefore are not included below. This list represents a conservative estimate of the true native reptile diversity within each island group as we did not include currently undescribed taxa, and considered a species introduced if a previous worker indicated the distribution was likely the result of an introduction and provided supporting data. Endemic species have a distribution restricted to a single archipelago. We used published literature (published prior to 1 August 2008), personal field observations, and unpublished molecular data to develop this list; the primary source(s) for each record is included with the record and references are provided below the table. Abbreviations are as follows: E=Endemic, N=Native, I=Introduced.

Taxon	Solomon Islands	Fiji Archipelago	Vanuatu Archipelago	Samoan Islands	Tongan Archipelago	New Caledonia	Loyalty Islands
AGAMIDAE							
Hypsilurus godeffroyi	N (1)						
DIPLODACTYLIDAE							
Bavayia crassicollis						N (18)	N (18)
Bavayia cyclura						N (18)	N (18)
Bavayia exsuccida						E (18)	
Bavayia geitaina						E (18)	
Bavayia goroensis						E (2)	
Bavayia madjo						E (18)	
Bavayia montana						E (18)	
Bavayia ornate						E (18)	
Bavayia pulchella						E (18)	
Bavayia robusta						E (18)	
Bavayia sauvagii						E (18)	N (18)
Bavayia septuiclavis						E (18)	
Dierogekko inexpectatus						E (19)	
Dierogekko insularis						E (19)	
Dierogekko kaalaensis						E (19)	
Dierogekko koniambo						E (19)	

Table A. cont.

Dierogekko nehoueensis						E (19)	
Dierogekko poumensis						E (19)	
Dierogekko thomaswhitei						E (19)	
Dierogekko validiclavis						E (19)	
Eurydactylodes agricolae						E (20)	
Eurydactylodes symmetricus						E (18)	
Eurydactylodes vieillardi						E (18)	
Oedodera marmorata						E (21)	
Rhacodactylus auriculatus						E (18)	
Rhacodactylus chahoua						E (18)	
Rhacodactylus ciliatus						E (18)	
Rhacodactylus leachianus						E (18)	
Rhacodactylus sarasinorum						E (18)	
Rhacodactylus trachyrhynchus						E (18)	
GEKKONIDAE							
Cyrtodactylus biordinis	E (1)						
Cyrtodactylus louisiadensis	N (1)						
Cyrtodactylus salomonensis	E (28)						
Gehyra mutilata	I (3,4)	I (3,4)	I (3,4)	I (3,4,27)			
Gehyra oceanica	N (1)	N (5,6)	N (10,11)	N (27)	N (10)		
Gehyra vorax	N (1)	N (5,6)	N (10,11)		N (10)	N (18)	N (18)
Gekko vittatus	N (1)		N (11)				
Hemiphyllodactylus typus	N (1)	N (5,6)	N (10)		N (10)	N (18)	I (26)
Lepidodactylus euaensis					E (10)		
Lepidodactylus flaviocularis	E (1)						
Lepidodactylus gardineri		E (5,6)					
Lepidodactylus guppyi	N (1)						
Lepidodactylus manni		E (5,6)					
Lepidodactylus mutahi	E (1)						
Lepidodactylus shebae	E (1)						

Table A. cont.

Lepidodactylus vanuatuensis			E (11,12)				
Nactus multicarinatus	N (1)		N (10,11, 13)				
Nactus pelagicus	N (1)	N (5,6)	N (10,11, 13)	N (27)	N (10)	N (18)	
Perochirus guentheri			E (10)				
IGUANIDAE							
Brachylophus fasciatus		N (5,6)			N (10)		
Brachylophus vitiensis		E (5,6)	I (10)				
SCINCIDAE							
Caledoniscincus aquilonius						E (18)	
Caledoniscincus atropunctatus			N (11,14)			N (18)	N (18)
Caledoniscincus auratus						E (18)	
Caledoniscincus austrocaledonicus						N (18)	N (18)
Caledoniscincus chazeaui						E (18)	
Caledoniscincus cryptos						E (18)	
Caledoniscincus festivus						E (18)	
Caledoniscincus haplorhinus						N (18)	N (18)
Caledoniscincus orestes						E (18)	
Caledoniscincus renevieri						E (18)	
Caledoniscincus terma						E (18)	
Carlia fusca	N (1)						
Corucia zebrata	E (1)						
Cryptoblepharus eximius		N (5,6,7)					
Cryptoblepharus novocaledonicus						N (7,18)	N (7,18)
Cryptoblepharus novahebridicus			E (10,11)				
Cryptoblepharus poeciloplerus	N (1)			N (27)	N (10)		
Emoia adspersa				E (27)			
Emoia aneityumensis			E (10,11,15)				
Emoia atrocostata	N (1)		N (10,11,15)				
Emoia caeruleocauda	N (1)	I (6)	N (10,11,15)				

Table A. cont.

Emoia campbelli		E (5,6)					
Emoia concolor		N (5,6)					
Emoia cyanogaster	N (1)		N (10,11,15)				
Emoia cyanura	N (1)	N (5,6)	N (10,11,15)	N (15,27)	N (10,15)		N (26)
Emoia erroran			E (10,11,15)				
Emoia flavigularis	E (1)						
Emoia impar	N (1)	N (5,6)	N (11,16,17)	N (15,27)	N (10,15)		
Emoia isolata	E (1)						
Emoia jakati	N (1)						
Emoia lawesii				N (15,27)	N (10,15)		
Emoia loyaltiensis							E (26)
Emoia maculata	E (1)						
Emoia mokosariniveikau		E (5,6)					
Emoia nigra	N (1)	N (5,6)	N (10,11,15)	N (15,27)	N (10,15)		
Emoia nigromarginata			E (10,11,15)				
Emoia parkeri		E (5,6)					
Emoia pseudocyanura	E (1)						
Emoia renellensis	E (1)						
Emoia rufiabialis	E (1)						
Emoia samoensis				E (15,27)			
Emoia sanfordi			E (10,11,15)				
Emoia schmidti	E (1)						
Emoia taumakoensis	E (1)						
Emoia tongana				N (27,28)	N (10,15)		
Emoia trossula		N (5,6)			N (10)		
Eugongylus albofasciolatus	E (1)						
Eugongylus rufescens	E (1)						
Geomyersia glabra	E (1)						
Geoscincus haraldmeieri						E (18)	
Graciliscincus shonae						E (18)	
Kanakysaurus viviparus						E (22)	

Table A. cont.

Lacertoides pardalis					E (18)	
Lamprolepis smaragdina	N (1)					
Leiolopisma alazon		E (5,6)				
Lioscincus greeri					E (18)	
Lioscincus maruia					E (18)	
Lioscincus nigrofasciolatus					N (18)	N (18)
Lioscincus novaecaledoniae					E (18)	
Lioscincus steindachneri					E (18)	
Lioscincus tillieri					E (18)	
Lioscincus vivae					E (23)	
Lipnia noctua	N (1,8,9)	I (8,9)	I (8,9,11)	I (8,9)		
Celatiscincus euryotis					E (24)	
Celatiscincus similes					E (24)	
Marmorosphax montana					E (18)	
Marmorosphax tricolor					E (18)	
Nannoscincus exos					E (18)	
Nannoscincus garrulous					E (25)	
Nannoscincus gracilis					E (18)	
Nannoscincus greeri					E (18)	
Nannoscincus hanchisteus					E (18)	
Nannoscincus humectus					E (18)	
Nannoscincus manautei					E (23)	
Nannoscincus mariei					E (18)	
Nannoscincus rankini					E (18)	
Nannoscincus slevini					E (18)	
Phoboscincus bocourti					E (18)	
Phoboscincus garnieri					N (18)	N (18)
Prasinohaema virens	N (1)					
Sphenomorphus bignelli	E (1)					
Sphenomorphus concinnatus	E (1)					
Sphenomorphus cranei	E (1)					

Table A. cont.

Sphenomorphus fragosus	E (1)		
Sphenomorphus solomonis	N (1)		
Sphenomorphus tanneri	E (1)		
Sphenomorphus taylori	E (1)		
Sphenomorphus transversus	E (1)		
Sphenomorphus woodfordi	E (1)		
Sigaloseps deplanchei			E (18)
Sigaloseps ruficauda			E (18)
Simiscincus aurantiacus			E (18)
Tachygia microlepis		E (10)	
Tribolonotus blanchardi	E (1)		
Tribolonotus ponceletti	E (1)		
Tribolonotus pseudoponceletti	E (1)		
Tribolonotus schmidti	E (1)		
Tropidoscincus aubrianus			E (18)
Tropidoscincus boreus			E (18)
Tropidoscincus variabilis			E (18)
VARANIDAE			
Varanus indicus	N (1)		

Primary references for data in Appendix 1: (1) McCoy 2006; (2) Bauer et al. 2008; (3) Fisher 1997; (4) Beckon 1992; (5) Morrison 2003; (6) Zug 1991; (7) Unpublished molecular data suggest *Cryptoblepharus eximius* (Fiji) and *C. novocaledonicus* (New Caledonia and Loyalty Islands) are conspecific; neither, therefore, is considered endemic; (8) Austin 1999a; (9) Austin 1999b; (10) Allison 1996; (11) Hamilton, field surveys; (12) Ota et al. 1998; (13) Zug and Moon 1995; (14) Bauer et al. 1992; (15) Brown 1991; (16) Bruna et al. 1995; (17) Bruna et al. 1996; (18) Bauer and Sadlier 2000; (19) Bauer et al. 2006; (20) Aaron Bauer, personal communication; (21) Sadlier et al. 2004a; (22) Sadlier et al. 2004b; (23) Sadlier et al. 2006a; (24) Sadlier et al. 2006b; (25) Sadlier and Bauer 1997; (26) Gill 1993a; (27) Zug and Gill 1997; (28) Rosler et al. 2007.

APPENDIX 2: PERMISSION FROM *ECOGRAPHY*

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VITA

Alison Madeline Hamilton was born in 1973, in Tallahassee, Florida, to Donna Lynn McCue Hamilton and Frank Eugene Hamilton, III. She grew up in Tampa, Florida, and attended Tampa Preparatory High School. As a child, her interest in the outdoors was encouraged by fishing trips with her father and grandfather and weekend canoeing and hiking trips with her godfather and his wife, Frank and Barbara Maloney. After completing 10th grade, Alison started college at Simon's Rock College of Bard, in Great Barrington, Massachusetts. While at Simon's Rock, Alison developed an interest in biology, ecology, and evolution through courses taught by Dr. Bob Schmidt, Dr. David Meyers, and Dr. Don Roeder. She had the opportunity to travel to Guyana, South America, to study cichlid fish with Drs. Schmidt and Roeder, and was employed by these two professors as a field research assistant during her junior and senior years in college. She conducted her senior thesis research on habitat use of two species of turtles under the advisement of Dr. Schmidt, and graduated with a Bachelor of Arts in natural science, with a concentration in ecology. She then moved to Seattle, Washington, where she worked as an environmental educator for the Pacific Science Center. In 2000, she received a Master of Science degree from the Department of Wildlife Ecology and Conservation from the University of Florida in the research group of Dr. C. Kenneth Dodd, Jr. She then moved to Grand Forks, North Dakota, to begin her doctoral research in the lab of Dr. Christopher Austin. In 2003, she moved to Louisiana State University with Dr. Austin when he accepted a position in the Museum of Natural Sciences and Department of Biological Sciences.